Zootaxa 2902: 1–43 (2011)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Multi-locus phylogeny and taxonomic revision of *Uperoleia* toadlets (Anura: Myobatrachidae) from the western arid zone of Australia, with a description of a new species

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Abstract

We generated a multi-locus phylogeny to test monophyly and distributional limits in Australian toadlets of the genus *Uperoleia* from the western arid zone of Australia. The molecular data were used in combination with a detailed assessment of morphological variation and some data on call structure to complete a taxonomic revision of the species that occur in this region. Our work reveals the existence of not two but five species in the region. *Uperoleia russelli* is restricted to the Carnarvon and Gascoyne Regions south of the Pilbara. *Uperoleia micromeles* is distributed from the Tanami Desert through the Great Sandy Desert and along the northern edge of the Pilbara. *Uperoleia talpa* was previously believed to be a Fitzroyland region endemic but it is further distributed along Dampierland and into the Roebourne Plain. *Uperoleia glandulosa* is a larger species than previously described as well as a greater habitat generalist, inhabiting the rocky Pilbara region and the sandy region around Port Hedland. We also describe a new species, *U. saxatilis* **sp. nov.**, endemic to the Pilbara craton.

Key words: frog, anuran, Pilbara, Kimberley, geology

Accepted by M. Vences: 9 Feb. 2011; published: 1 Jun. 2011

Introduction

Uperoleia Gray, 1841 is the most species diverse frog genus in the Australo-Papuan endemic family Myobatrachidae, currently comprising 26 described species (Cogger 2000; Doughty & Roberts 2008). This morphologically conservative genus is comprised of small (2–4 cm), squat and short-limbed frogs with drab brown ground color. They display conspicuous skin glands that may be highlighted with cream, orange, or gold pigment. They also typically display a femoral color patch that may be yellow, orange, or red depending on the species. Advertisement calls are simple, consisting of rasps, squelches, or clicks (Tyler *et al.* 1981). Commonly referred to as 'toadlets' or 'gungans', *Uperoleia* species are distributed primarily in the monsoonal regions across northern Australia and in temperate eastern Australia, but a number of species have adapted to more arid regions.

Previous studies of the Pilbara region of Western Australia have identified a large number of regional endemics including several mammals and a large number of reptiles (Morton *et al.* 1995; Pepper *et al.* 2006; Smith & Adams 2007; Doughty *et al.* 2010). A recent study by Powney *et al.* (2010) found that Australian reptile species richness was highest in dry and hot regions, including the western arid zone, and that reptile species richness was largely uncorrelated with that of other vertebrates. An analysis of anuran endemism and species richness did not find the western arid zone to be an area of significant endemism in any Australian frog families (Slatyer *et al.* 2007). Likewise, a continent-wide study of plant species also did not find the western arid zone to be an area of high endemism (Crisp *et al.* 2001). These conflicting results regarding regional endemism could suggest taxon-specific influences on speciation in the western arid zone or, as acknowledged as possible by Slatyer *et al.* (2007) and Crisp *et al.* (2001), that results in the western arid zone were affected by a combination of poor sampling, poorly understood species distributions, and cryptic species.

At present, two species of *Uperoleia* are recognized from the western arid zone: *U. russelli* Loveridge, 1933 and *U. glandulosa* Davies, Mahony, and Roberts, 1985. *Uperoleia russelli* is described as a medium-sized robust species with short limbs, conspicuous glands, extensively webbed toes and has a squelch as an advertisement call (Tyler *et al.* 1981; Tyler & Doughty 2009). *Uperoleia glandulosa* is also a medium-sized species but differs from *U. russelli* by having reduced webbing between the toes, well-developed skin glands that connect along the sides, and an advertisement call that is a sharp 'click' (Davies *et al.* 1985). The currently understood distribution of *U. russelli* covers the entire Pilbara craton and extends into the Carnarvon and Gascoyne Regions, whereas *U. glandulosa* is more narrowly distributed along the northern coastal region of the Pilbara near Port Hedland and also further inland along the Yule River (Tyler & Doughty 2009).

Recent surveys of the Pilbara and surrounding regions have resulted in a substantial increase in voucher specimens and tissue samples, which provided an opportunity to reevaluate *Uperoleia* diversity. Preliminary examination of morphology suggested greater diversity than reflected in the current taxonomy, with the southern Carnarvon and Gascoyne region *U. russelli* populations appearing to have a different dorsal pattern compared to individuals from the Pilbara. In their description of *U. glandulosa*, Davies *et al.* (1985) reported hearing a third kind of *Uperoleia* call from the northern coastal region but were not able to collect any specimens. We also found morphologically unusual specimens in the northern coastal regions not attributable to either *U. russelli* or *U. glandulosa.*

Monophyly of *Uperoleia* has never been questioned and a multi-locus phylogeny of all myobatrachid frog species provides strong support (J.S. Keogh *et al.* unpublished data). While a few *Uperoleia* species have been included in various phylogenetic studies (Blake 1973; Roberts & Watson 1993; Read *et al.* 2001; Frost *et al.* 2006), none focused specifically on relationships within the genus. We generated a multi-locus phylogeny for all members of the genus specifically to examine relationships and ranges of *Uperoleia* species distributed in the arid regions of northwestern Australia (Fig. 1). We also analyzed the morphology, advertisement calls, and distributions of taxa from the Pilbara and surrounding regions to resolve the systematics of *Uperoleia* species, clarify distributions, and redescribe or describe all known species from the region.

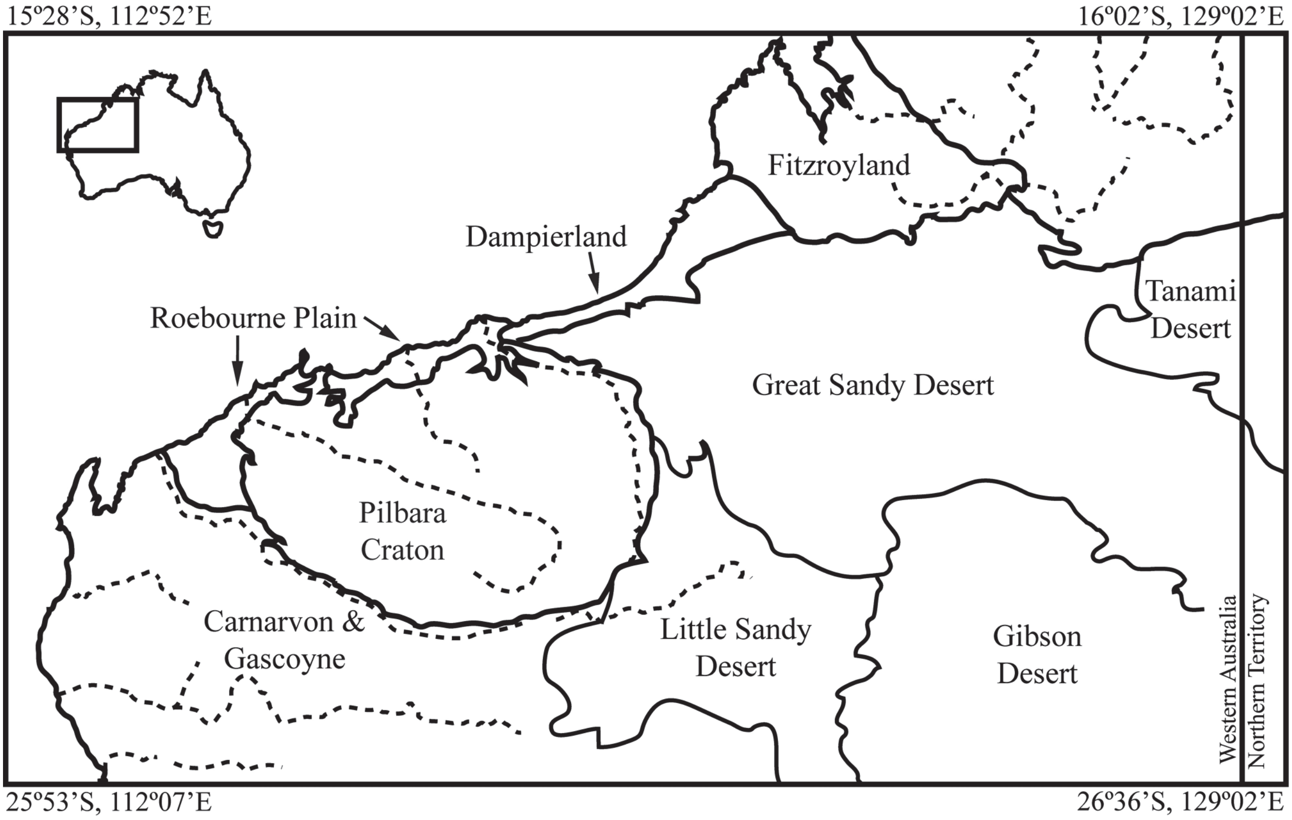

FIGURE 1. Geological regions of the western arid zone of Australia. Solid lines denote geological boundaries and dotted lines represent rivers. Modified from Beard & Webb (1974), Beard (1975, 1979), and Interim Biogeographic Regions of Australia version 6.1 (Commonwealth of Australia 2005).

Methods

Molecular methods

Choice of tissues and phylogenetic markers. We generated sequence data for all available western arid zone *Uperoleia* material available from the major Australian frozen tissue collections (Appendix 1). We also included a representative of most described *Uperoleia* species to assess the relationships of the western arid zone taxa and to provide the as yet most comprehensive phylogeny for the genus (Appendix 1). We excluded *U. arenicola, U. capitulata, U. daviesae, U. martini, U. marmorata*, *U. mimula,* and *U. orientalis,* either due to lack of tissue samples or taxonomic uncertainty, but none of these species inhabits the western arid zone.

We used a two-step strategy to obtain phylogenetic information. First, we generated sequence data for two mitochondrial DNA (mtDNA) genes (16S and ND2) for all samples included in this study (Genbank Accession details in Appendix 2). Second, based on these results, we selected three representatives of all recovered clades of the target species, and one individual for all other described species. For these samples we also generated sequence data for three protein coding nuclear DNA (nDNA) genes (POMC, RAG-1, and BDNF) to provide additional independent datasets to test species monophyly. The genes 16S, ND2, POMC, and RAG-1 have been used extensively in anuran studies (Gamble *et al.* 2000; Chari *et al*. 2004; Darst & Cannatella 2004; Evans *et al*. 2003; Hoegg *et al.* 2004; Crawford & Smith 2005; van der Meijden *et al.* 2005; Garda & Cannatella 2007; Morgan *et al.* 2007; Guarnizo *et al.* 2009; Matsui *et al.* 2010; Thome *et al.* 2010). BDNF also has been phylogenetically informative in other similar studies (Noonan & Chippindale 2006; Raxworthy *et al.* 2008; Adalsteinsson *et al.* 2009).

Molecular protocols. Total genomic DNA was extracted from liver or toe tissue using a cetyltrimethyl ammonium bromide (CTAB) method, suspended in TE and stored at -4°C. Loci were amplified using primers and protocols in Table 1 and resulted in the amplification of a single band. Negative controls were run in every experiment to

test for contamination. Sequencing followed Pepper *et al.* (2006). Sequences were assembled using Sequencher 4.8 (Genes Codes Corporation), aligned with the program eBioX 1.5.1 (eBioinformatics) using the default settings for Clustal W (Thompson *et al.* 1994), and adjusted manually.

TABLE 1. PCR primers and amplification profiles.

Region	Primer	**Sequence (5'–3')**	PCR Profile	Source
Ribosomal large sub-unit (16S)	L16Sc H16Sd	GTRGGCCTAAAAGCAGCCAC CTCCGGTCTGAACTCAGATCAC	(94°C for 30 s, 50°C for 30 s, 72°C for 1 min) x 30	Evans *et al.* 2003 Modified from Evans *et al.* 2003
NADH dehydro-genase-2 (ND2)	L4221 L4437 HND2 tRNA-asn	AAGGRCCTCCTTGATAGGGA AAGCTTTCGGGGCCCATACC CTTCTACTRKCGGCTTTGAA CTAAAATRTTRCGGGATCGAG	(94°C for 30 s, 55°C for 30 s, 72°C for 1 min) x 30	Macey *et al.* 1998 Macey *et al.* 1998 This study Read *et al.* 2001
Recombination activating gene 1 (RAG-1)	AMP-Rag1F AMP-Rag1R1	AGCTGCAGYCARTACCA-YAARATGTA AACTCAGCTGCATTKCCAATRT-CACA	(95C for 15 s, 55C for 15 s, 72C for 30 s) x 2, (95C for 15 s, 54C for 15 s, 72C for 30 s) x 2, (95C for 15 s, 53C for 15 s, 72C for 30 s) x 2, (95C for 15 s, 52C for 15 s, 72C for 30 s) x 2, (95C for 15 s, 51°C for 15 s, 72°C for 30 s) x 2, (95°C for 15 s, 50°C for 15 s, 72°C for 30 s) x 30	San Mauro *et al.* 2007 San Mauro *et al.* 2007
Proopiomelano-cortin (POMC)	POMC-F1 POMC-R1	ATATGTCATGASCCAYTTYCGCT-GGAA GGCRTTYTTGAAWAGAGTCATT-AGWGG		Vietes *et al.* 2004 Vietes *et al.* 2004
Brain-derived neurotrophic fac-tor (BNDF)	BDNF_Fmb BDNF_Rmb	GACCATCCTTTTCCTKACTATG-GTTATTTCATACTT CTATCTTCCCCTTTTAATGGT-CAGTGTACAAAC		Modified from Vietes *et al.* 2004 Modified from Vietes *et al.* 2004

Molecular analysis. For both the mtDNA and combined mt/nDNA data sets, phylogenetic trees were estimated using maximum parsimony (MP) and Bayesian inference (BI). *Spicospina flammocaerulea* was used as an outgroup in all analyses as it represents the monotypic sister genus to *Uperoleia* (Read *et al.* 2001; J.S. Keogh, unpublished data). Parsimony analysis was performed using PAUP* version 4.0b (Swofford 2003) using a heuristic search under equal weighting of all characters (1000 random stepwise addition and TBR branch swapping). The number of trees saved during the searches was not restricted. Gaps were treated as missing data. Non-parametric bootstrap resampling was used to evaluate branch support (1000 replicates).

Bayesian inference of gene phylogenies was carried out with BEAST (version 1.5.3, Drummond & Rambaut 2007) using the GTR+Γ+I substitution model in a partitioned Bayesian analysis under a relaxed clock model (Drummond *et al.* 2006). Each gene represented one partition. Model parameter values were treated as unknown and estimated during the run. Separate genes were treated as unlinked to obtain separate parameter estimates of each. Each Markov chain was independently run three times starting from a random tree. For the mtDNA analysis the Monte Carlo Markov chain length was 10,000,000 and trees were sampled every 1000 generations. For the combined mtDNA and nDNA analysis the chain length was 20,000,000 and trees sampled every 2000 generations. The first 10% of sampled trees were discarded as burn-in and convergence of the Bayesian runs was checked with Tracer 1.5 (Rambaut & Drummond 2007). Trees sampled after this burn-in were used to determine posterior probabilities of model parameters, branch lengths, and clade support.

Morphological and distributional data

We examined specimens from the Western Australian Museum (WAM) as well as paratypes of *U. micromeles* from the South Australian Museum (SAMA) (Appendix 1). We aimed to include 20 specimens of each target clade as identified by genetic results in the morphometric analyses. We preferentially included specimens for which we also had genetic data. If there were not 20 specimens available with genetic data then we measured well-preserved specimens without available tissue but were identifiable based on morphology and location. Where available, both male

and female specimens were examined and we preferentially used adult specimens from different collection locations (Appendix 1).

We measured the following morphological characters: snout-urostyle length (SUL), eye-naris distance (EN—from anterior corner of the eye to midpoint of closest nostril), interorbital distance (IO—from anterior corners), internarial distance (IN—from medial margins of nares), eye length (EyeL—from corner of anterior and posterior edges), arm length (ArmL—from elbow to tip of 3rd finger), tibia length (TL), and foot + tarsus length (from knee to tip of 4th toe). Extent of fronto-parietal fontanelle exposure was determined as per Tyler *et al.* (1981). 'Narrowly exposed' is used where the maximum extent of exposure is less than 10% of maximum skull width and 'extensively exposed refers' to exposure of approximately 20% of maximum skull width. Where paratypes were unavailable for examination and previous studies found a maximum or minimum value outside the extent of ours, we quote those details in the taxonomy section. Previous authors have used the extent of webbing between the toes as a taxonomic character in *Uperoleia*, but the character was not always consistently described. We quantified the extent of webbing between the toes and identified four categories relative to tubercles (see Fig. 2). Sex was determined in the field at the time of collection (male if frog was calling or had heavily pigmented chin and nuptial pad, females if obviously gravid), or by dissection in the lab.

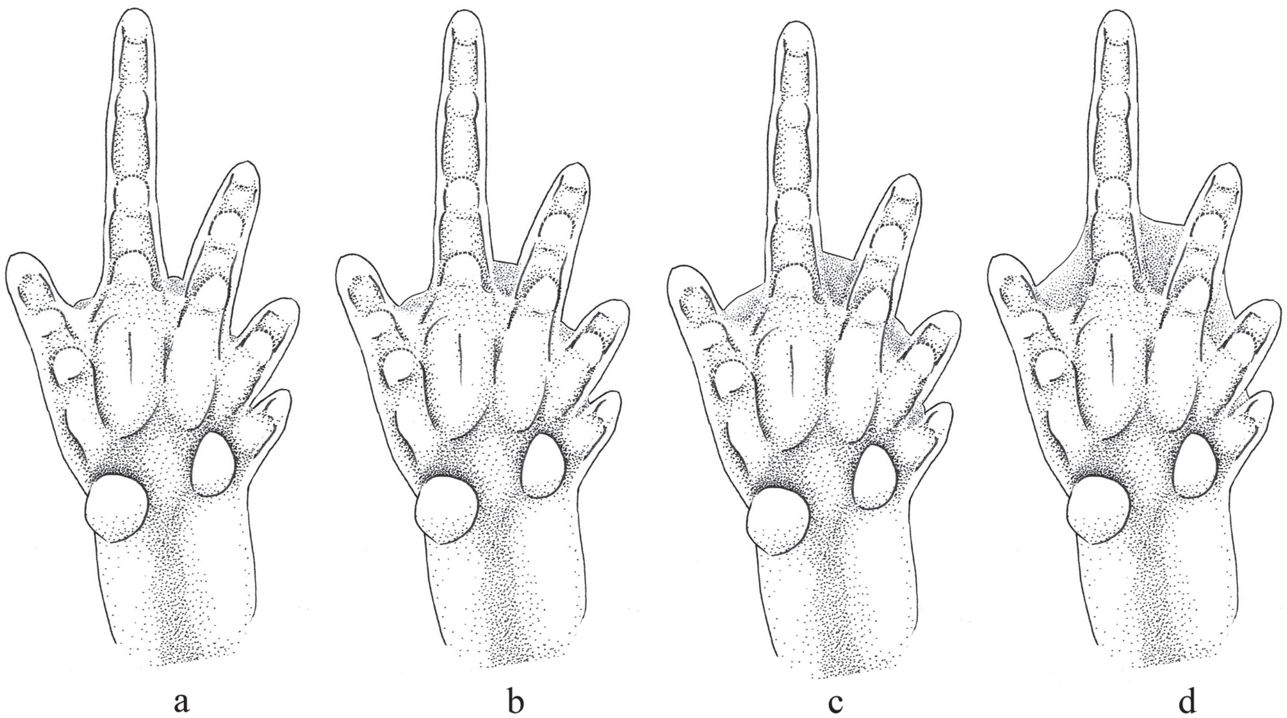

FIGURE 2. Extent of webbing relative to tubercle position on the fourth toe. a) basal webbing, b) webbing extends to the first proximal tubercle, c) webbing extends to halfway between the first and second proximal tubercles, d) webbing extends to the second proximal tubercle.

We used Principal Components Analysis (PCA), which does not identify groups *a priori*, and Discriminant Function Analysis (DFA), where the genetic clades were specified *a priori*, to examine the patterns of relationship among all nine morphological characters (natural log transformed) with the statistics software JMP 8.0. As not all specimens could be measured for all characters, we calculated standard principal components with variance-covariance and imputation of missing values so that all 113 animals could be included in the PCA. Analyses based on non-imputed data gave the same result (not shown). The first principal component was interpreted as representing variation in body size and shape and the second principal component summarized shape differences among the clades. We then performed DFA on the ln-transformed data to examine if body shape differences would be sufficient to distinguish species when they were specified *a priori*.

Once morphometric measurements were completed, the remaining vouchers available at the WAM were sorted by morphology into each of the five taxa our integrative data supported (see Results) in order to provide additional distributional data. Fewer specimens of *U. micromeles* have been collected due to their distribution in some of the

most inaccessible areas of Australia. To provide more detailed information on this species we also included distributional data from the Northern Territory Museum (NTM) and Northern Territory field surveys. *Uperoleia micromeles* is morphologically highly distinct from other *Uperoleia* so field survey identifications are likely to be accurate.

Call recording and analysis

We obtained recordings for two *U. glandulosa* (recordings same as Davies *et al.* 1985), three *U. saxatilis* **sp. nov.** (described below, recording of holotype,WAM R162877, and two unvouchered individuals from Snake Creek in Millstream-Chichester National Park), three *U. talpa* (WAM R161205-6 and one unvouchered individual from Tabba Tabba Creek near Marble Bar Rd Junction), and five unvouchered *U. russelli* from the Gascoyne River Bridge at Carnarvon. No calls for *U. micromeles* were available for analysis. Digital recordings were made using Marantz PMD 660 digital recorders and with either Beyer M88 or AKG D880m microphones. *Uperoleia glandulosa* calls were recorded on a Sony TC-510-2 reel-to-reel tape recorder with an AKG D190 or Beyer M101 microphone and digitized by playback into a Marantz PMD 660 digital recorder. All unvouchered calls were recorded using a Zoom H2 digital recorder. Calls were analyzed using Raven Pro 1.3. We measured call and pulse duration to the nearest ms. Frequency was analyzed using a Hann window, 1024 samples and we selected the peak frequency from a spectrum display. For each call we measured duration, pulse number, pulse rate (averaged over whole call), and dominant frequency also averaged over the whole call. We have reported a whole call average for ease of comparison. Air temperature was measured at the calling site for frogs calling on land but water temperature for species calling in water.

Results

Molecular analyses

In total 2047 base pairs (bp) of mtDNA sequence data were obtained for 111 specimens. The edited alignment of 16S comprises 760 bp of which 21.2% were parsimony informative and ND2 comprised 1287 bp of which 33.0% were parsimony informative. An additional 2105 bp of nDNA sequence data were obtained for representatives of mtDNA clades. The edited alignment of RAG-1 comprised 819 bp of which 5.4% were parsimony informative, POMC comprised 584 bp of which 7.2% were parsimony informative, and BNDF comprised 702 bp of which 3.4% were parsimony informative. In total there were 4152 bp in the combined analysis.

The topologies derived from the parsimony and Bayesian analyses of the combined 16S and ND2 mtDNA data (Fig. 3) and the multi-gene (16S, ND2, POMC, BNDF, Rag-1) data (Fig. 4) were highly concordant. Therefore, the description of the phylogeny and taxonomic revision focuses on the combined multi-locus data set (Fig. 4) with reference to the mtDNA tree (Fig. 3) where relevant to distribution.

The combined analysis yielded strong support for four species groups within *Uperoleia* (Fig. 4). Species from the western arid zone are members of three of these clades and do not form a monophyletic group. *Uperoleia glandulosa* is within clade 1, *U. micromeles* is within clade 2, and *U. russelli*, *U. talpa*, and an additional clade distributed in the arid zone are all within clade 3.

Clade 1 is comprised of the species *U. altissima, U. aspera, U. glandulosa, U. littlejohni, U. lithomoda, U. minima, U. rugosa,* and *U. trachyderma* (PP = 1). Each individual species within this clade is strongly supported in both the mtDNA and mt/nDNA phylogenies (PP ≥ 0.92). This clade is represented by species distributed widely across Australia, including the arid zone species *U. glandulosa*, the widespread monsoonal tropics species *U. lithomoda* and *U. trachyderma*, the northwestern Kimberley region endemic *U. minima* and the Fitzroyland species *U. aspera*. This group is sister to a clade (PP ≥ 0.91) represented by the Cape York endemics *U. littlejohni* and *U. altissima*, and the inland New South Wales and southwest Queensland species *U. rugosa*. The relationship between these two larger clades has strong support (PP = 1.0). The placement of *U. glandulosa* within this speciose clade has strong support (PP ≥ 0.99). Tissues in the *U. glandulosa* clade were collected from the eastern Roebourne Plain and the Yule River of the Pilbara craton (Fig. 8a).

Clade 2 is comprised of *U. micra, U. micromeles,* and *U. mjobergii* (PP = 1). The sister relationship of *U. mjobergii*, a Fitzroyland endemic, and *U. micromeles* is strongly supported (PP = 1). The small *U. micra,* a Kimberley endemic, is the sister taxon to the *U. micromeles/U. mjobergii* clade (PP = 1). The placement of *U. micromeles* with two of the smallest species is strongly supported (PP = 1). Tissues in the *U. micromeles* clade were collected from across the extreme sandy arid zone including the Tanami and Great Sandy Deserts (Fig. 8b).

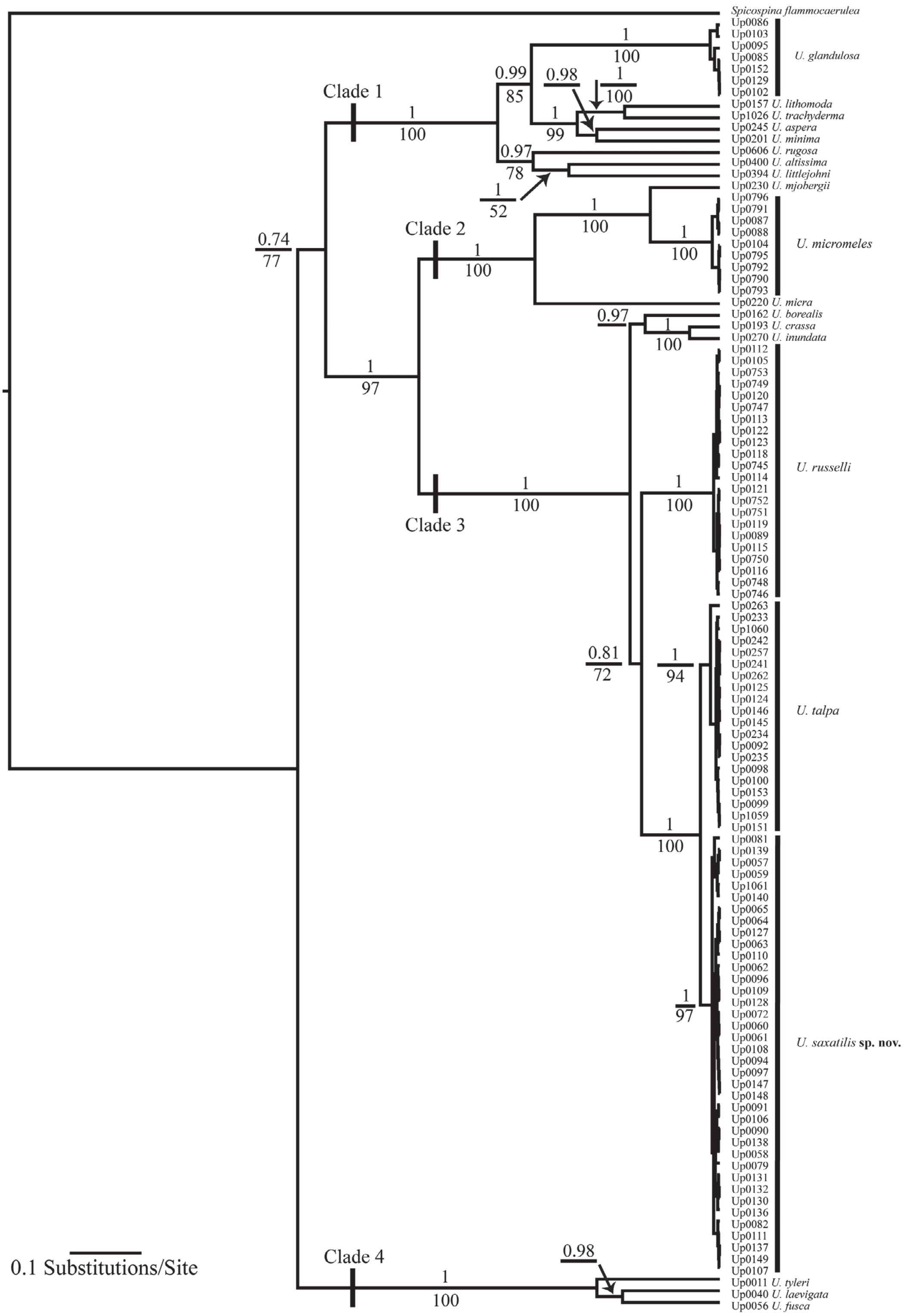

FIGURE 3. Molecular phylogeny of the genus *Uperoleia* based on the mtDNA genes 16S and ND2 (total 2,047 bp), including all tissues available for sequencing from the western arid zone. The phylogeny shown is based on a partitioned Bayesian analysis where each gene represents one partition. Values above the branches are Bayesian posterior probabilities and values below are the parsimony bootstrap values.

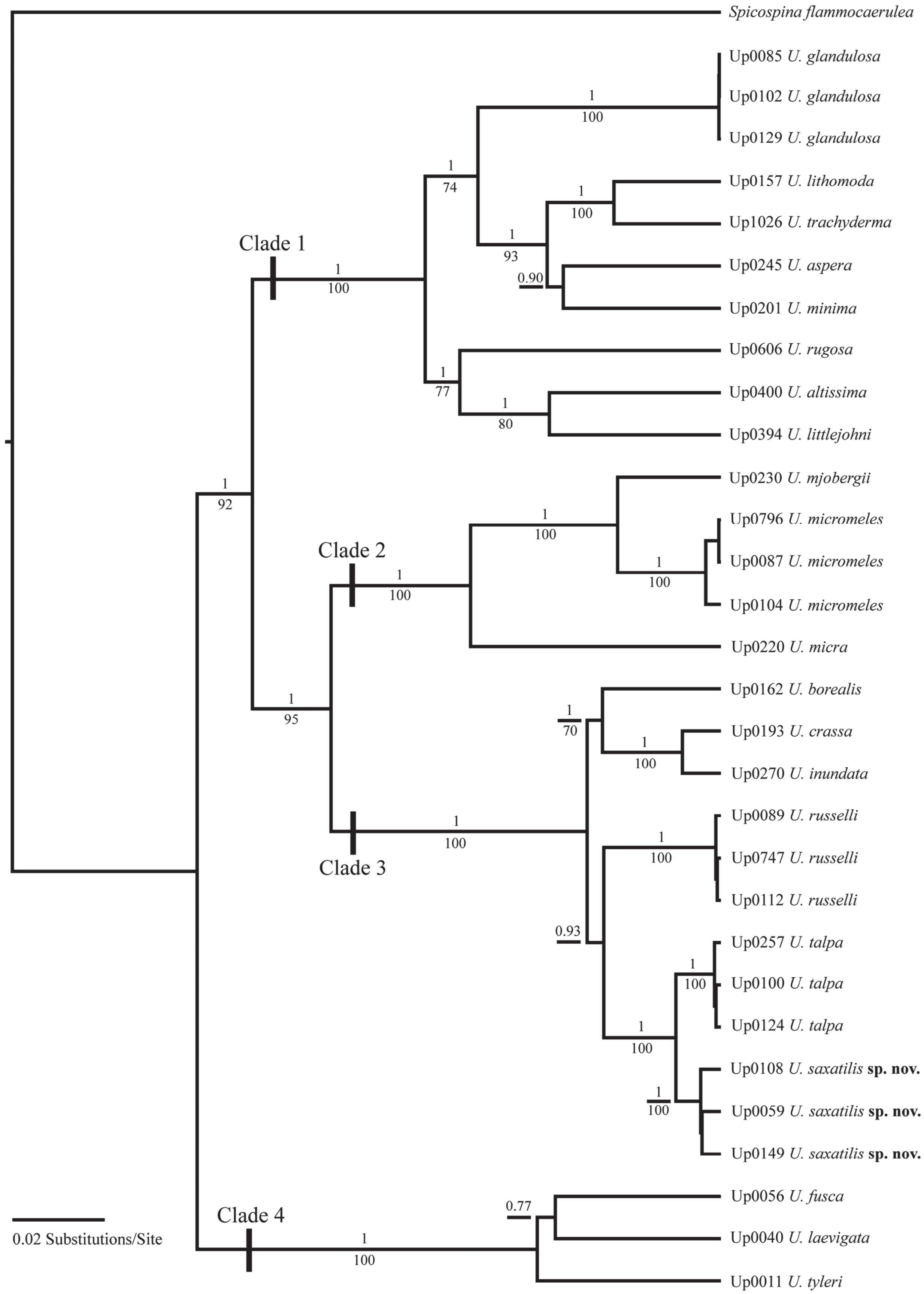

FIGURE 4. Molecular phylogeny of the genus *Uperoleia* based on a combined analysis of five genes including the mtDNA genes 16S and ND2 and the nuclear loci RAG-1, POMC, and BNDF (total 4,152 bp). The phylogeny shown is based on a partitioned Bayesian analysis, see text for details. Values above the branches are Bayesian posterior probabilities and values below are the parsimony bootstrap values.

TABLE 2. Intraspecific genetic divergence within each of the five target species and interspecific genetic divergences between each of the five target species and its sister taxon. Both uncorrected and corrected distances are shown. Number of individuals used from each clade is noted below the divergence value.

Intraspecific genetic divergence

Taxon	ND2 uncorrected	ND2 corrected (GTR+I+G)	16S uncorrected	16S corrected (GTR+I+G)	Combined nDNA uncorrected	Combined nDNA corrected (GTR+I+G)
U. glandulosa	0.00–0.009 N = 7	0.00–0.010 N = 7	0.00–0.008 N = 7	0.00–0.008 N = 7	0.00–0.001 N = 3	0.00–0.001 N = 3
U. micromeles	0.00–0.009 N = 9	0.00–0.009 N = 9	0.00–0.003 N = 9	0.00–0.001 N = 9	0.00–0.0005 N = 3	0.00–0.0005 N = 3
U. saxatilis **sp. nov.**	0.00–0.011 N = 38	0.00–0.013 N = 38	0.00–0.008 N = 38	0.00–0.011 N = 38	0.00–0.001 N = 3	0.00–0.001 N = 3
U. russelli	0.00–0.008 N = 22	0.00–0.008 N = 22	0.00–0.002 N = 22	0.00–0.002 N = 22	0.000 N = 3	0.000 N = 3
U. talpa	0.00–0.012 N = 20	0.00–0.011 N = 20	0.00–0.012 N = 20	0.00–0.004 N = 20	0.00–0.0015 N = 3	0.00–0.0015 N = 3

Interspecific genetic divergence

Taxon Comparison	ND2 uncorrected	ND2 corrected (GTR+I+G)	16S uncorrected	16S corrected (GTR+I+G)	Combined nDNA uncorrected	Combined nDNA corrected (GTR+I+G)
U. glandulosa and *U. lithomoda*	0.125–0.129 N = 7, 1	0.181–0.185 N = 7, 1	0.053–0.057 N = 7, 1	0.060–0.066 N = 7, 1	0.007–0.008 N = 3,1	0.007–0.008 N = 3,1
U. micromeles and *U. mjobergii*	0.047–0.071 N = 9, 1	0.054–0.088 N = 9, 1	0.023–0.026 N = 9, 1	0.024–0.027 N = 9, 1	0.001–0.002 N = 3,1	0.001–0.002 N = 3,1
U. saxatilis **sp. nov.** and *U. russelli*	0.059–0.076 N = 38, 22	0.071–0.096 N = 38, 22	0.019–0.040 N = 38, 22	0.020–0.043 N = 38, 22	0.002 N = 3,3	0.002 N = 3,3
U. saxatilis **sp. nov.** and *U. talpa*	0.017–0.028 N = 38, 20	0.017–0.030 N = 38, 20	0.002–0.012 N = 38, 20	0.002–0.013 N = 38, 20	0.005–0.007 N = 3,3	0.005–0.008 N = 3,3

Clade 3 is comprised of the species *U. russelli, U. talpa , U. borealis, U. crassa*, *U. inundata*, and an additional clade (PP = 1). Our samples from the rocky Pilbara craton, previously assigned to *U. russelli*, showed a close sister relationship to *U. talpa*. Although the branch lengths are short, genetic evidence shows strong support for divergence in both mtDNA and combined mt/nDNA analyses (both PP=1). Sequencing showed fixed differences between *U. talpa* and the sister clade in all five loci. Specimens located on the Pilbara craton consistently were identified to the new clade that we hereafter refer to and describe below as *U. saxatilis* **sp. nov.** Specimens from the Roebourne Plain and Fitzroyland were consistently identified to the *U. talpa* clade (Fig. 8d).

Both the mtDNA and combined mt/nDNA analyses strongly support the *U. russelli* clade (PP = 1), which is restricted to the Carnarvon and Gascoyne sandplains (Fig. 8c). The clade comprising the western monsoonal tropics species *U. borealis, U crassa,* and *U. inundata* is strongly supported at all nodes (PP = 1).

Clade 4 comprised *U. fusca, U. laevigata*, and *U. tyleri* (PP = 1), all of which are only known to occur on the eastern side of the Great Dividing Range on the east coast of Australia.

Corrected intraspecific genetic divergences (Table 2a) in each clade are small. The *U. saxatilis* **sp. nov.** intraspecific genetic divergences are greatest at a maximum of 1.3% in ND2, followed by *U. talpa* with a maximum of 1.1% intraspecific divergence, *U. glandulosa* with 1.0%, *U. micromeles* with 0.9%, and *U. russelli* with 0.8%. Levels of intraspecific genetic divergence in 16S follow similar patterns as ND2 except that *U. glandulosa* shows greater intraspecific divergence than *U. talpa* (0.8% *versus* 0.4%). The percentage of intraspecific divergence in the combined nuclear gene dataset is less than 0.1% for all five arid zone clades. In all cases the maximum intraspecific genetic divergence is less than the minimum interspecific divergence to the nearest sister clade.

Minimum genetic divergence between pairs of key species (*U. glandulosa* and *U. lithomoda*, *U. micromeles* and *U. mjobergii, U. saxatilis* **sp. nov.** and *U. russelli,* and *U. saxatilis* and *U. talpa)* are presented in Table 2b. The corrected genetic divergences between *U. saxatilis* **sp. nov.** and *U. talpa* are small for mtDNA (1.7% in ND2, 1.3% in 16S), but monophyly of these clades is also strongly supported by the nuclear DNA data sets (0.5% divergence).

Morphology

Table 3 presents the results of the morphological comparisons of the five western arid zone species. *Uperoleia glandulosa* appears to be the smallest of the species present in the region, reaching a maximum size of ~30 mm SUL. It also has generally longer feet (FL/SUL = 0.64±0.05 [0.57–0.74]) and has extensive skin glands that connect along the sides. A slightly larger size (males 20.9–33.0 mm, females 24.6–32.8 mm SUL *versus* males 20.5–30.4 mm, females 25.1–27.5 mm SUL) and large but unconnected skin glands distinguish *U. russelli* from *U. glandulosa*. *Uperoleia russelli* also has more extensive webbing (Fig. 2d) between the toes than *U. glandulosa* (Fig. 2b).

The most distinctive of all the *Uperoleia* in this region is *U. micromeles*. This species is the second largest of the *Uperoleia* and has slightly shorter arms and feet (ArmL/SUL = 0.39±0.02 [0.35–0.43], FL/SUL = 0.58±0.02 [0.55–0.63]) than other western arid zone *Uperoleia*. Of note is that this is the only species where the distance between the nostrils is larger than the distance between the eye and nostril (i.e. EN/IN < 1) so it has a wide, blunt snout. This is also the only species in the western arid zone with basal toe webbing (Fig. 2a). *Uperoleia talpa* and the closely related *U. saxatilis* **sp. nov.** are morphologically similar, but are distinguishable on body size (males 23.7–36.1 mm, females 24.2–40.8 mm SUL *versus* males 24.0–33.3 mm, females 27.4–36.6 mm SUL) and foot length (FL/SUL = 0.57±0.04 [0.47–0.69] *versus* FL/SUL = 0.60±0.04 [0.54–0.68]) and snout shape (EN/IN = 1.32±0.13 [1.09–1.66]) *versus* EN/IN = 1.40±0.12 [1.18–01.66]), although identification may require a combination of characters. *Uperoleia talpa* is larger, has shorter legs, and a blunter snout than *U. saxatilis* **sp. nov.**

PCA demonstrated that *U. micromeles* and *U. talpa* differ substantially in body proportions from the other three species. *U. russelli* and *U. saxatilis* **sp. nov.** are indistinguishable in body proportions based on the PCA analysis and *U. glandulosa* differs marginally from these two. These results were evident in plots of both PCA 1 *versus* PCA 2 (Fig. 5) and PCA *2 versus* PCA 3 (not shown). Despite the considerable overlap in body proportions among these three taxa (Table 3), DFA, in which species identity was known *a priori*, was able to correctly identify 96% of the specimens to species (Fig. 5). Importantly, these analyses were restricted to body size and proportions, but several other key characters such as gland shape and size, color patterning, and toe webbing are diagnostic of species.

TABLE 3. Summaries of characters and ratios measured for *Uperoleia*. Mean±St.Dev. (range). Total sample sizes are listed in column headings followed by the sample size of each gender (M for male, F for female, T for combined).

Character	*U. glandulosa* N = 17 (M = 12, F = 5)	*U. micromeles* N = 9 (M = 3, F = 6)	*U. russelli* N = 20 (M = 14, F = 6)	*U. talpa* N = 29 (M = 19, F = 10)	*U. saxatilis* **sp. nov.** N = 23 (M = 16, F = 7)
SUL	M: 24.8±2.6 (20.5–30.4) F: 25.1±1.8 (22.8–27.5)	M: 29.8±1.2 (28.8–31.1) F: 28.2±5.6 (22.2–37.6)	M: 28.7±3.0 (20.9–33.0) F: 28.9±2.8 (24.6–32.8)	M: 32.1±3.3 (23.7–36.1) F: 34.4±4.7 (24.2–40.8)	M: 28.2±3.0 (24.0–33.3) F: 31.9±3.2 (27.4–36.6)
TL	M: 9.4±0.6 (8.4–10.4) F: 8.9±0.8 (2.8–9.9)	M: 10.5±0.6 (9.9–10.9) F: 10.0±1.6 (8.4–12.6)	M: 10.0±0.9 (7.2–11.2) F: 9.9±0.9 (8.9–11.2)	M: 10.5±0.7 (8.7–11.4) F: 11.2±1.4 (8.6–13.1)	M: 10.1±1.1 (8.6–12.0) F: 10.6±1.0 (9.3–12.0)
FTL	M: 15.9±0.9 (14.5–17.3) F: 15.7±0.8 (15.1–16.9)	M: 17.4±0.6 (16.9–18.0) F: 16.3±3.3 (12.9–20.9)	M: 17.3±1.6 (13.2–19.0) F: 17.9±1.9 (15.4–20.8)	M: 18.2±1.5 (15.6–20.6) F: 19.3±2.4 (14.6–22.7)	M: 17.3±1.6 (14.0–19.8) F: 18.3±1.5 (16.4–20.4)
ArmL	M: 10.6±0.9 (9.4–12.6) F: 10.2±1.6 (8.4–12.2)	M: 11.4±0.43 (10.9–11.7) F: 11.0±1.7 (8.9–13.3)	M: 11.0±1.2 (9.3–13.9) F: 12.2±1.3 (10.2–13.9)	M: 13.3±1.3 (10.8–15.6) F: 14.2±1.7 (11.0–6.3)	M: 11.7±1.0 (9.9–13.3) F: 12.2±1.6 (9.4–14.0)
IO	M: 4.4±0.3 (4.0–4.9) F: 4.3±0.4 (3.8–4.8)	M: 5.5±0.1 (5.4–5.6) F: 5.1±1.0 (4.2–6.7)	M: 4.7±0.5 (3.4–5.4) F: 4.8±0.4 (4.3–5.4)	M: 5.2±0.4 (4.5–5.8) F: 5.5±0.6 (4.6–6.3)	M: 4.7±0.4 (4.1–5.4) F: 5.1±0.5 (4.3–5.7)
EyeL	M: 2.8±0.5 (1.5–3.4) F: 2.7±0.2 (2.6–2.9)	M: 3.3±0.2 (3.2–3.5) F: 3.2±0.7 (2.8–3.8)	M: 2.8±0.2 (2.3–3.1) F: 2.2±0.1 (2.1–3.1)	M: 3.4±0.3 (2.8–3.9) F: 4.1±1.3 (2.9–4.3)	M: 2.9±0.2 (2.5–3.4) F: 3.1±0.3 (2.6–3.5)
EN	M: 2.2±0.3 (1.9–2.9) F: 2.1±0.3 (1.8–2.5)	M: 2.3±0.1 (2.2–2.4) F: 2.1±0.4 (1.6–2.5)	M: 2.3±0.2 (1.8–2.6) F: 2.2±0.1 (2.1–2.3)	M: 2.4±0.2 (2.0–2.8) F: 2.5±0.3 (2.0–3.1)	M: 2.3±0.2 (2.0–2.6) F: 2.5±0.2 (2.2–2.8)
IN	M: 1.7±0.2 (1.4–2.0) F: 1.7±0.2 (1.5–1.9)	M: 2.7±0.1 (2.7–2.8) F: 2.4±0.5 (1.9–3.3)	M: 1.7±0.2 (1.3–1.9) F: 1.7±0.1 (1.5–1.9)	M: 1.8±0.1 (1.5–2.0) F: 2.0±0.2 (1.6–2.3)	M: 1.7±0.2 (1.3–2.1) F: 1.8±0.1 (1.6–2.0)
TL/SUL	M: 0.38±0.03 (0.33–0.42) F: 0.36±0.01 (0.34–0.37) T: 0.37±0.03	M: 0.35±0.02 (0.34–0.37) F: 0.36±0.02 (0.33–0.38) T:0.36±0.01	M: 0.35±0.02 (0.33–0.39) F: 0.35±0.03 (0.31–0.39) T: 0.35±0.02	M: 0.33±0.02 (0.29–0.38) F: 0.33±0.01 (0.31–0.36) T: 0.33±0.02	M: 0.36±0.02 (0.33–0.39) F: 0.33±0.02 (0.31–0.36) T: 0.35±0.02
FL/SUL	M: 0.65±0.06 (0.57–0.74) F: 0.63±0.02 (0.61–0.66) T: 0.64±0.05	M: 0.58±0.01 (0.58–0.59) F: 0.58±0.03 (0.55–0.63) T: 0.58±0.02	M: 0.61±0.03 (0.54–0.70) F: 0.62±0.07 (0.53–0.70) T: 0.61±0.04	M: 0.57±0.05 (0.47–0.69) F: 0.56±0.02 (0.53–0.60) T: 0.57±0.04	M: 0.62±0.04 (0.54–0.68) F: 0.58±0.03 (0.54–0.61) T: 0.60±0.04
ArmL/SUL	M: 0.43±0.04 (0.38–0.50) F: 0.41±0.03 (0.37–0.44) T: 0.40±0.11	M: 0.38±0.02 (0.37–0.40) F: 0.39±0.02 (0.35–0.43) T: 0.39±0.02	M: 0.42±0.02 (0.39–0.47) F: 0.42±0.04 (0.38–0.47) T: 0.42±0.03	M: 0.42±0.02 (0.37–0.45) F: 0.41±0.02 (0.38–0.45) T: 0.41±0.02	M: 0.39±0.11 (0.39–0.47) F: 0.38±0.03 (0.34–0.42) T: 0.39±0.09
EN/IN	M: 1.28±0.11 (1.09–1.39) F: 1.24±0.13 (1.03–1.36) T: 1.27±0.11	M: 0.85±0.03 (0.82–0.88) F: 0.88±0.11 (0.70–0.98) T: 0.87±0.09	M: 1.36±0.08 (1.24–1.60) F: 1.32±0.05 (1.24–1.6) T: 1.35±0.08	M: 1.35±0.10 (1.17–1.61) F: 1.25±0.15 (1.09–1.66) T: 1.32±0.13	M: 1.40±0.13 (1.18–1.66) F: 1.40±0.11 (1.21–1.58) T: 1.40±0.12

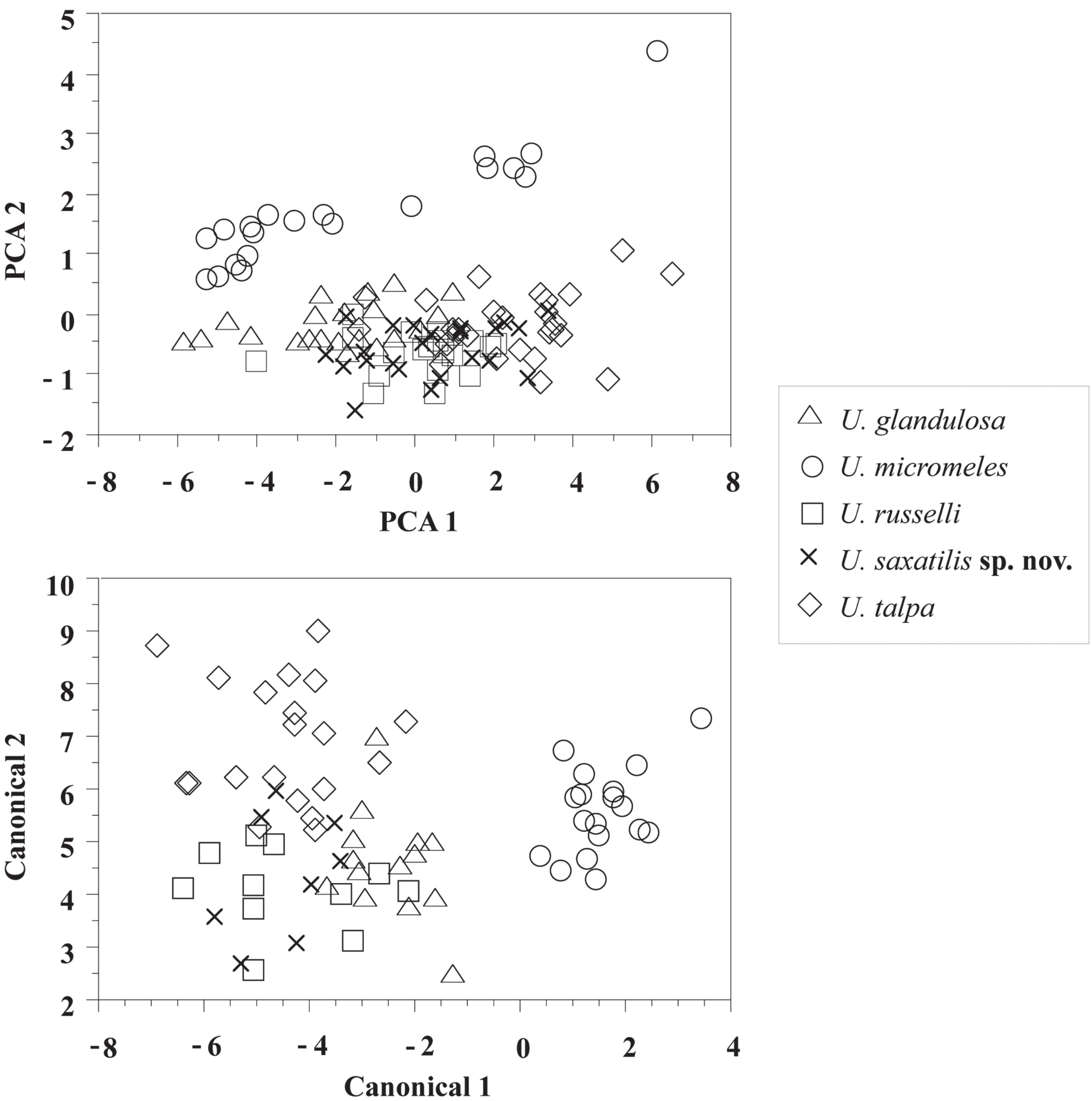

FIGURE 5. Plot showing results of Principle Components Analysis (top) and Discriminant Function Analysis (bottom) on body proportion variables only, see text for details. *Uperoleia micromeles* is the most distinct and *U. russelli* and *U. saxatilis* **sp. nov.** are indistinguishable based on these characters, but each is distinct based on genetic, call and other morphological characters.

Advertisement calls

Northwestern *Uperoleia* calls sound like clicks or squelches depending on the number and rate of pulses. Table 4 summarizes the main features of calls. Oscillograms and sound spectrograms are presented in Fig. 6. The call of *U. glandulosa* (Fig. 6a) is a short sharp click: a single note formed by two to four pulses (Davies *et al.* 1985).

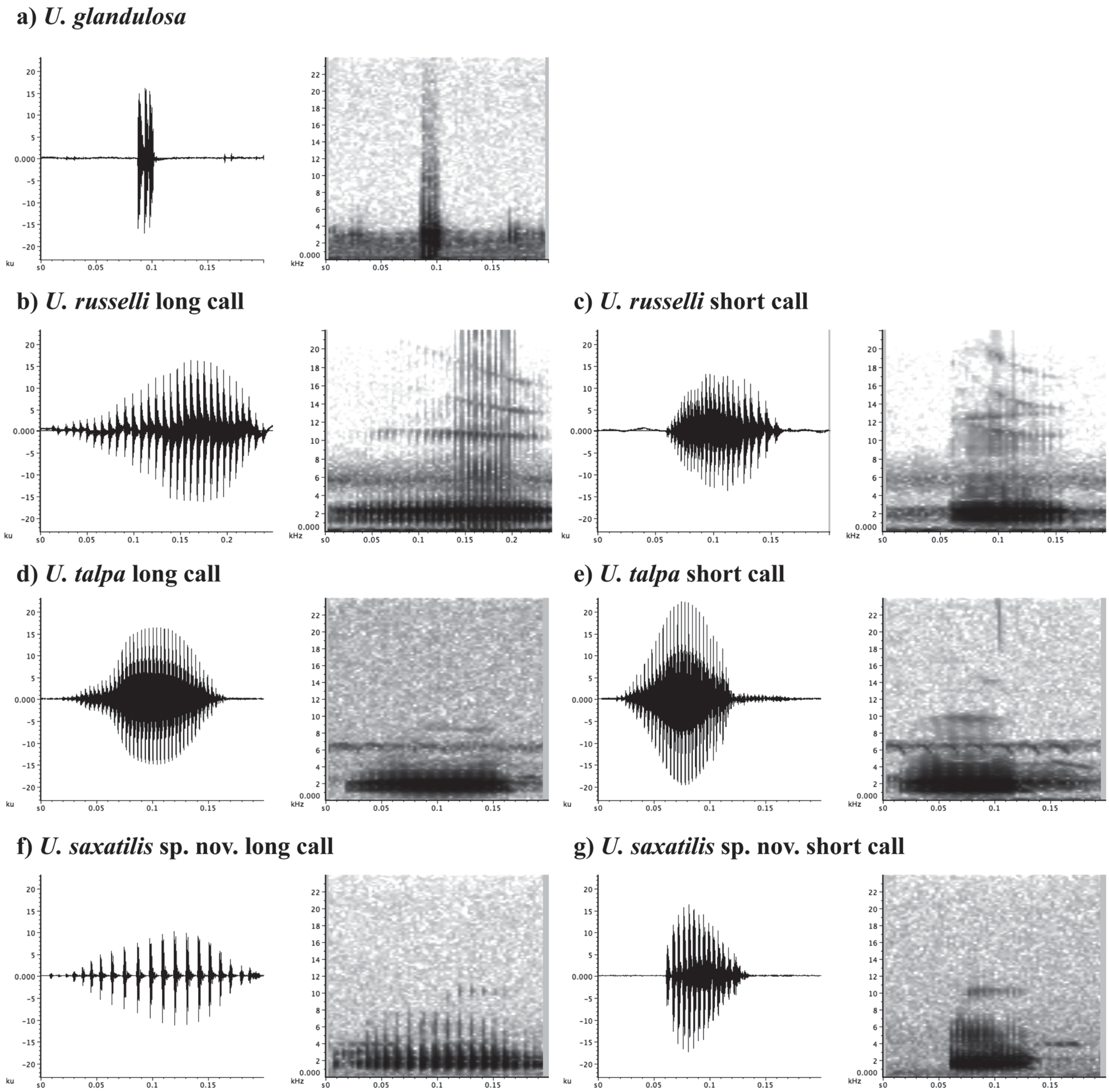

FIGURE 6. Oscillographs and spectrograms of (a) *U. glandulosa*, *U. russelli* (b) long call and (c) short call, *U. talpa* (d) long call and (e) short call, and *U. saxatilis* **sp. nov.** (f) long call and (g) short call.

The five individuals in the *U. russelli* recordings had a relatively long squelch as a call, and two of the individuals were recorded intermittently using a second shorter call. The *U. russelli* long call (Fig. 6b) is an extended squelch formed by 22 to 38 pulses, where four individuals had averages of approximately 30 pulses per call, a small individual had an average of 22 pulses per call, and a large individual intermittently had a pulse number of 38. Each pulse had up to 18 oscillations, and a slow decay to approximately 1/4 peak amplitude before the next pulse was initiated. Pulse durations were equal to the pulse period (about 7 ms). Average call duration was 20 ms. The second call (Fig. 6c) heard in the call sequence of two *U. russelli* individuals is a short squelch formed by 17 to 27 pulses, where the smaller individual averaged 18 pulses and a larger individual averaged 26 pulses. This call has a shorter duration than the first call (average of 12 ms). A unique characteristic of this call is the reduction in pulse rate over the length of the call. The pulse rate for pulses 2 to 4 average 274 pulses/s, reducing to an average 135 pulses/s for the fourth to second final pulses. This reduction in pulse rate can be seen clearly in Fig. 6c.

Two different calls were recorded from specimens of *U. talpa*. The first call of *U. talpa* was a short squelch formed by 27 to 28 pulses (Fig. 6e). Each pulse had seven oscillations, a quick decay to 1/2 the peak amplitude and

a slow decay to approximately 1/4 peak amplitude before the next pulse was initiated. Pulse durations were equal to the pulse period (about 3 ms). This short call has a long tail of low amplitude pulses that was approximately 1/3 of total call time and can be seen in Fig. 6e. The *U. talpa* ‘long’ call was a squelch of approximately 29 to 44 pulses (Fig. 6d). Each pulse had seven oscillations and a slow decay to approximately 1/3 peak amplitude before the next pulse was initiated. Pulse durations were equal to the pulse period (approximately 3 ms). Due to the lack of ‘tail’ in this call, the easily humanly audible portion of the ‘long’ call is longer than that of the ‘short’ call (0.12 s versus 0.08 s).

TABLE 4. Call structure characters in western arid zone *Uperoleia* (Mean [St.]). Similar calls with different temperatures are listed separately where temperature has had a strong affect on pulse rate. M = Male.

	Duration (ms)	Dominant Frequency (Hz)	Pulses/s	Pulses/call	Temp (ºC)
U. glandulosa					
N= 13 calls from 2 M	1.5 [0.002]	3097.6 [94.8]	173.7 [17.5]	2.54 [0.52]	25
U. russelli (long)					
N = 20 calls from 5 M	20 [0.01]	2261.0 [43.0]	152.3 [9.7]	25.1 [2.9]	27
U. russelli (short)					
N = 8 calls from 2 M	12.1 [0.01]	2320.2 [96.1]	see text	22 [4.1]	27
U. talpa (long)					
N = 10 calls from 2 M	12.6 [1.5]	1992.2 [24.7]	266.3 [4.6]	33.5 [4.1]	26.4
N = 4 calls from 1 M	11.8 [0.01]	2607.2 [0]	357.5 [26.0]	41.7 [1.7]	31.5
U. talpa (short)					
N = 4 calls from 1 M	8.8 [0.005]	2132.8 [27.0]	313.3 [19.6]	27.5 [0.6]	25.9
U. saxatilis (long)					
N = 9 calls from 1 M	21.6 [2.1]	1562.5 [27.1] or 2140 [24]	99.2 [4.4]	21.3 [1.4]	23
N = 8 calls from 2 M	13.7 [0.08]	1744.2 [30.4] or 2239.5 [0]	153.63 [9.9]	21 [1.2]	34.7
U. saxatilis (short)					
N = 22 calls from 1 M	7.9 [1.2]	1556.5 [53.2] or 2121 [49.5]	213.5 [23.5]	16.7 [1.6]	23
N = 2 calls from 1 M	7.5 [0.006]	1765.7 [0.0]	258.8 [12.4]	19.5 [0.7]	34.7

The holotype of *U. saxatilis* **sp. nov.** and an individual from Snake Creek each displayed two different calls. The ‘long’ call recorded in all three individuals was a drawn out squelch formed by 19–24 pulses (Fig. 6f). The pulses had four to five oscillations and a quick decay to null amplitude before the next pulse is initiated. Pulse durations (about 7 ms) are shorter than the pulse periods (about 11 ms). The call duration between the two locations appears highly affected by the 11ºC difference in temperature, with the call duration reduced by approximately 8 ms at the higher temperature. The ‘short’ call of *U. saxatilis* **sp. nov.** is a fast squelch consisting of 15–20 pulses (Fig. 6g). The pulses have five or six oscillations and an irregular decay to approximately ¼ of the peak amplitude before the next pulse is initiated. Pulse periods are approximately 2.7 ms and are equal to the pulse duration. At the higher temperature location, call duration remains similar but the average number of pulses per call is increased *versus* the lower temperature location. Both the ‘long’ and ‘short’ *U. saxatilis* **sp. nov.** calls had two peak frequencies. The first peak is at approximately 1594 kHz and the second is at 2125 kHz. While both peaks exist simultaneously in all calls, the dominant frequency varies between call bouts. These dual bands are visible in the spectrograms in Fig. 6.

Taxonomy

The combined genetic, morphological, and call data provides strong evidence for the presence of five evolutionary lineages representing species in the western arid zone. Four of these lineages have been previously described. Our molecular data provides strong evidence for the assignment of vouchers to specific species and thus enabled the

development of strongly supported diagnoses for each species, which are redescribed below. The fifth lineage is genetically, morphologically, and acoustically divergent from all other described species of *Uperoleia*, and we describe it below as *U. saxatilis* **sp. nov.** An identification key to the five species in the region is included in Table 5.

TABLE 5. Taxonomic key to western arid zone *Uperoleia.*

1.	Distance between nostrils greater than distance between nostril and anterior corner of eye; pale tubercles on upper edge of snout	***U. micromeles***
	Distance between nostrils is smaller than distance between nostril and anterior corner of eye	**2**
2.	Inguinal glands long, thin, and possibly connecting to the parotoid gland; large, bright flash coloration present at groin	**3**
	Inguinal glands highly reduced or absent and usually restricted to the posterior of the body; pale and reduced or no flash coloration present at groin	**4**
3.	Dark paravertebral stripes above parotoid glands, posterior portion of dorsal surface covered by irregular dark patches; toes webbed to first proximal tubercle; call is a sharp click	***U. glandulosa***
	Dark blotches on dorsal surface, often interconnecting, form paravertebral stripes that extend down length of dorsal surface and do not break up into irregular patches; toes webbed to second proximal tubercle; call is a squelch	***U. russelli***
4.	Toes webbed to between first and second proximal tubercle; Dorsal surface is bronze with sparse light brown spots, usually topped with a reddish tubercle; Call length is approximately 8.8 ms with 27–28 pulses per call or call length is approximately 12.6 ms with 33.5 pulses per call including a long ‘tail’ of short pulses; present in sandy regions of the Roebourne Plain, Dampierland, and Fitzroyland	***U. talpa***
	Toes webbed to between first and second proximal tubercles or to the second proximal tubercle; Dorsal surface is brown with many irregular dark brown spots; Call length is approximately 21.6 ms with 21.3 pulses per call or call length is approximately 7.9 ms with 16.7 pulses per call; present in rocky gorges on the Pilbara Craton	***U. saxatilis* sp. nov.**

Uperoleia Gray, 1841

Uperoleia Gray, 1841, Ann. Mag. Nat. Hist., Ser. 1, 7: 90.
Hyperoleia Agassiz, 1846, Nomencl. Zool., Fasc. 12: 384. Unjustified emendation.
Glauertia Loveridge, 1933, Occas. Pap. Boston Soc. Nat. Hist., 8: 89. Type species: *Glauertia russelli* Loveridge, 1933, by monotypy. Synonymy by Tyler *et. al.* 1981, Aust. J. Zool., Suppl. Ser., 29 (79): 9.
Hosmeria Wells and Wellington, 1985, Aust. J. Herpetol., Suppl. Ser., 1: 2. Type species: *Uperoleia marmorata laevigata* Keferstein, 1867, by original designation.
Prohartia Wells and Wellington, 1985, Aust. J. Herpetol., Suppl. Ser., 1: 3. Type species: *Pseudophryne fimbrianus* Parker, 1926, by original designation.
Type species: *U. marmorata*, by monotypy.

Diagnosis. A group of small-bodied (to 41 mm) terrestrial frogs with short limbs, no webbing on fingers, first finger shorter than second, inner metatarsal tubercle not compressed, lacking vomerine teeth, covered tympana, pupil rhomboidal, parotoid, dorsolateral/inguinal and coccygeal glands usually present, males with unilobular submandibular vocal sac and unpigmented nuptial pads, aquatic reproduction with small pigmented eggs and free-swimming larvae (Tyler *et al.* 1981). Cloacal flap present, moderately fimbriated in males and strongly fimbriated in females.

Other genera in synonymy. *Uperoleia* are morphologically conservative and monophyly is not in question based on morphological (Tyler *et al*., 1981) or molecular data (Read *et al*., 2001; Frost *et al*., 2006, this study). Parker (1940) indicated *Hyperoleia* was an unjustified emendation of *Uperoleia*. There are no compelling reasons to recognize further genera within this clade. Therefore we maintain the synonymy of *Glauertia* by Tyler *et. al.* (1981) and tranfer *Hosmeria* and *Prohartia* to the synonymy of *Uperoleia.*

Uperoleia glandulosa Davies, Mahony, and Roberts, 1985
Glandular Toadlet

Uperoleia glandulosa Davies, Mahony, and Roberts, 1985, Trans. R. Soc. S. Aust. 109: 103

Holotype. WAM R89489, adult male collected at Petermarer Creek, Port Hedland-Broome Rd, WA (21º23'6"S, 118º48'21"E) on 10 January 1983 by M. Mahony and J.D. Roberts.

Paratypes. There are seven paratypes, six adult males and one adult female: WAM R89490–2, AMS R114573 collected with the holotype; SAMA R27081–2 (cleaned and stained), 3.2 km NE Wittenoom turnoff on Port Hedland-Broome Rd, WA, on 10 January 1983 by M. Mahony and J.D. Roberts; WAM R22921, Mundabullangana (5 km E of homestead), WA, on 19 Feb 1961 by G.M. Storr.

Diagnosis. Distinguished from congeners by a combination of small body size (males 20.6–30.4 mm, females 22.8–27.5 mm SUL) with moderately long limbs (TL/SUL 0.37±0.03 [0.33–0.42]), narrow snout (EN/IN 1.28±0.11 [1.03–1.47]), absence of maxillary teeth, extensively exposed frontoparietal fontanelle, faintly tubercular skin on dorsum, olive-brown dorsal surface with loosely connected irregular dark markings, orange femoral patches, well-developed parotoid, inguinal and coccygeal glands; inguinal gland thin and long, sometimes connecting to parotoid gland. Toes webbed to first or just past first proximal tubercles (Fig. 2b), and oval inner and broad outer metatarsal tubercles. A sharp 'click' as an advertisement call.

Description. Moderate body size, squat and rotund. Head small with slightly protruding eyes. When viewed laterally, evenly sloping snout with slightly rounded tip; when viewed from above, sides of snout gradually terminate in rounded point. Canthus rostralis prominent and rounded; loreal region sloping and slightly convex. Small and rounded medial projection (synthesis of mentomeckelian bones) that matches notch on upper jaw. Nostrils directed upwards; nares with a raised edge. Anterior corner of eye covered by flap of skin; at dorsal terminus the skin overlaps the skin of the brow above the eye. Tympana not visible, covered by skin and parotoid glands. Tongue oval and elongate. Maxillary and vomerine teeth absent. Frontoparietal fontanelle extensively exposed (Davies *et al.* 1985). EN larger than IN (EN/IN 1.27±0.11 [1.03–1.39]).

Arms and hands moderately built. Arms of moderate length (ArmL/SUL 0.40±0.11 [0.37–0.50]), fingers poorly fringed and unwebbed. Finger length 3>4>2>1. Tubercles under fingers extensively developed; one on first and second, two on third and fourth. Palmar tubercles large and prominent. Large outer palmar tubercle on distal portion of wrist. Nuptial pad of males on inner portion of first finger (beginning halfway down finger), extending to base of wrist (¼ along forearm) and slightly encroaching on palmar surface.

Legs moderately long (TL/SUL 0.37±0.03 [0.33–0.42]) and of thin build. Toe length 4>3>5>2>1. Tubercles under toes conical and well developed: one on first and second, two on third and fifth, three on fourth. Toes long, webbed to first or just beyond first proximal tubercles (Fig. 2b), and moderately to extensively fringed. Large oval inner metatarsal tubercle, oriented along fifth toe. Outer metatarsal tubercle large, rounded, spatulate, and oriented perpendicular to foot.

Dorsum faintly tubercular with a raised mid-vertebral line on snout extending posteriorly to between parotoid glands, and sometimes to urostyle. Tiny pale tubercles occasionally on either side of snout, especially below eye. Ventral surface slightly granular, with scattered white tubercles. Well developed parotoid, inguinal and coccygeal glands; inguinal long and thin, occasionally continuous with parotoid. Mandibular gland moderately developed but disrupted.

Coloration in life. Dorsal ground color pale to dark olive brown. An unbroken dark brown 'V' pointed posteriorly is located between the eyes, occasionally interrupted at midline by vertebral row of orange tubercles. Large dark semi-circular markings that curve above the parotoid glands usually present. Dorsal surface with loosely connected irregular dark brown blotches, including on glands (Fig. 7). All glands colored orange or yellowish-orange. Large red orange femoral patches and in groin. Ventral surface whitish and flecked with gray. Chest is occasionally unpigmented, and a few larger white tubercles are present at the junction of the arms and chest. Thighs are unpigmented with scattered white tubercles. Males have a darkly pigmented chin.

Advertisement call. Figure 6 summarizes the main features of the call. The call is a sharp click comprised of two to four pulses.

Habitat. Specimens have been collected from drainage lines with sparse tree cover and in roadside pools, and in ephemeral pools in riverbeds. Davies *et al.* (1985) report 'males were calling at the base of sedge clumps at the water's edge or in a similar position in the water' and 'around a flooded claypan'. As a microhabitat preference, we observed *U. glandulosa* preferred areas covered with thick sedge clumps close to water. Under the continuous cover of the grass *U. glandulosa* did not appear to hide under litter or otherwise attempt to conceal location.

Distribution. *Uperoleia glandulosa* is only known to occur along the eastern portion of the Roebourne Plain from Goldsworthy to Mundabullangana, and occurs inland along the Yule River in the Chichester subregion (Fig.

8a). The Roebourne Plain is characterized by a sandy substrate supporting coastal grasslands interspersed with floodplains. The area receives intermittent rainfall during summer.

Etymology. *glandulosa* refers to the conspicuous glands of this species.

Comparisons with other species. *Uperoleia glandulosa* is distinguished from other *Uperoleia* species in the western arid zone by a combination of characters including dark paravertebral bands above but not extending far posteriorly past the parotoid glands. *Uperoleia russelli* has dark longitudinal bands running down the full length of the body and *U. micromeles, U. saxatilis* **sp. nov.**, and *U. talpa* do not have dark dorsal bands. Glands are orangish and unlike all but *U. russelli* the glands usually connect along the sides. They have an extensively exposed frontoparietal fontanelle unlike all other western arid zone *Uperoleia*, and toe webbing extends to the first or just past the first proximal tubercle (Fig. 2b), which is more extensive than *U. micromeles* and less extensive than *U. russelli* and *U. saxatilis* **sp. nov.** Within the region, *U. glandulosa* is the only species known to have a short sharp click as an advertisement call.

Remarks. The original species description by Davies *et al.* (1985) contains detailed and accurate information. This species appears highly limited by geological boundaries including the rocky Pilbara craton to the south and the Great Sandy Desert to the northeast. The Roebourne Plain continues along the entire coastline of the Pilbara, except for the protrusion of the Chichester Range where it reaches the coast between Karratha and Roebourne. This rocky area may act as a barrier to further dispersal into the western Roebourne Plain for this species.

Uperoleia micromeles Tyler, Davies, and Martin, 1981
Tanami Toadlet

Uperoleia micromeles Tyler, Davies, and Martin, 1981 Aust. J. Zool., Suppl. Ser. 79: 46–49.

Holotype. SAMA R17175, an adult female collected in the Tanami Desert, Northern Territory, on 18 January 1978 by M. Gillam and I. Andrews. In the original description Tyler *et al.* (1981) note the coordinates as 28º38'S; 130º25'E. However, these coordinates contained a typo and the correct coordinates are 20º38'S; 130º25'E (M.J. Tyler, per. comm.).

Paratypes. There are five paratypes, one adult male and four adult females NTM R31199 (previously Central Australian Museum (CAMA) 140); SAMA R17176–78, R17221. All paratypes share the same collection details as the holotype.

Diagnosis. Distinguished from congeners by a combination of large body size (males 24.2–31.1 mm, females 22.2–37.6 mm SUL) with short to moderate length limbs (TL/SUL 0.36±0.01 [0.33–0.38]), very broad snout (EN/IN 0.87±0.09 [0.70–0.98]), absence of maxillary teeth, narrowly exposed frontoparietal fontanelle, scattered pale or reddish tubercles on dorsum, pale tubercles conspicuous on side of snout and above eyes, dull brown dorsal surface with irregular-shaped rich dark brown and red blotches, usually a vertebral row of orange tubercles from snout to urostyle, well developed parotoid and subarticular glands, inguinal and coccygeal glands moderately developed and restricted to rear of body. Toes basally webbed (Fig. 2a), and thin exceptionally large and projecting inner and outer metatarsal tubercles.

Description. Body large, squat, rotund, and thick. Head wide with small eyes. When viewed laterally, thick snout with little slope and squarish tip; when viewed from above, the sides of the snout slope minimally and end in a wide square tip. Canthus rostralis not defined; loreal region sloping and moderately concave. Rounded medial projection (synthesis of mentomeckelian bones) on lower jaw that matches notch on upper jaw. Nostrils directed upwards; nares with moderate rim. Anterior corner of eye moderately covered by flap of skin; at dorsal terminus the skin overlaps the skin of the brow above the eye. Posterior edge of brow projects slightly over skin on side of head. Tympana covered by skin and parotoid glands. Tongue oval and elongate. Maxillary and vomerine teeth absent. Frontoparietal fontanelle narrowly exposed (Tyler *et al.* 1981). EN less than IN (EN/IN 0.87±0.09 [0.70–0.98]).

Arms and hands thickly built. Arms are short (ArmL/SUL 0.39±0.02 [0.35–0.43]) and fingers are poorly fringed and unwebbed. Finger length 3>4=2>1. Tubercles under fingers moderately developed; one on first and second, two on third and fourth. Large outer palmar tubercle on distal portion of wrist. Nuptial pad of males on inner portion of first finger (beginning halfway down finger), extending to base of wrist (¼ along forearm) and slightly encroaching on palmar surface.

Figure 7: Photos in Life. Top row from left to right: *Uperoleia glandulosa* from Tabba Tabba Ck (M. Anstis), *U. micromeles* from South Headland (H. Cook), and *U. russelli* from Gascoyne River Crossing (M. Anstis). Bottow Row from left to right: *U. saxatilis* **sp. nov.** from Mt. Brockman (WAM R162771, P. Doughty), *U. saxatilis* **sp. nov.** from Mt. Brockman (WAM R162774, P. Doughty), and *U. talpa* from Tabba Tabba Ck (M. Anstis).

Legs short (TL/SUL 0.36±0.01 [0.33–0.38]) with thickly muscled tibia. Toe length 4>3>5>2>1. Tubercles under toes moderately developed; one on first and second, two on third and fifth, three on fourth. First toe extremely reduced and fifth toe very narrow (½ the width of the third toe). Toes basally webbed (Fig. 2a) and moderately to strongly fringed. Inner and outer metatarsal tubercles extremely large and spatulate, oriented perpendicular to the foot.

Dorsum with scattered tubercles, with a raised mid-vertebral stripe. Large pale tubercles present along snout above mouth. Ventral surface slightly granular. Parotoid gland well developed; inguinal and coccygeal glands moderately developed. Mandibular gland well developed, discrete and prominent posterior to angle of jaw.

Coloration. The dorsal surface is a pale dull brown, with irregularly connected dark brown and red blotches. A vertebral row of crimson tubercles runs from snout to cloaca, with scattered red tubercles on the eye, hind limbs, and glands. Scattered white tubercles occur above the mouth on the side of the snout. The parotoid glands are suffused with metallic gold (Fig. 7). Ventral and femoral coloration is unknown. Males have a darkly pigmented chin.

Advertisement call. Unknown.

Habitat. Occurs in sandridge deserts with Spinifex. Several specimens collected under rocks adjacent to creeks or pools. Known to burrow up to 2 m down in deserts during the dry season (Thompson *et al.* 2005).

Distribution. Widely distributed across the Tanami Desert of the Northern Territory and the Great and Little Sandy Deserts in Western Australia, extending to the north-eastern edge of the Pilbara craton near Port Hedland (Fig. 8b).

Etymology. *micromeles* is derived from the Greek *micros* (small) and *melos* (limb) referring to the short limbs of this species.

Comparisons with other species. *Uperoleia micromeles* is easily distinguished from all other *Uperoleia* species by the very broadly spaced nares. It is the only species where the internarial span is greater than the eye-naris distance (EN/IN 0.87±0.09 [0.70–0.98], all others EN/IN < 1). The basal toe webbing and pale spots on the side of the snout also serve as strong distinguishing characters when used in combination with the broadly spaced nares, as no other arid zone *Uperoleia* share these characteristics.

Remarks. The ability of this species to live within some of the driest and hottest areas in Australia is remarkable, and distributional information is potentially limited by the difficulty surveying sand dunes and remote locations during the monsoonal wet season when frogs may be active. This species may also be more extensively distributed in the Gibson Desert as it forms part of the Great Sandy Desert drainage (Beard & Webb 1974).

Uperoleia russelli (Loveridge, 1933)

Northwest Toadlet

Glauertia russelli Loveridge, 1933, Occas. Pap. Boston Soc. Nat. Hist., 8: 89.
Uperoleia russelli, Tyler, Davies and Martin, 1981 Aust. J. Zool., Suppl. Ser. 79: 19–24.

Holotype. WAM R2608, collected on the bank of Aurillia Creek flowing into the Gascoyne River near Landor Station (24º53'S, 116º59'E), Western Australia, by L. Glauert (collection date unknown, believed to be 1929).

Paratypes. There are 23 paratypes: Museum of Comparative Zoology, Harvard University (MCZ) 19424–9, SAMA R9723, WAM R2609–25. Paratype collection details as for holotype.

Diagnosis. Distinguished from congeners by a combination of moderate body size (males 20.9–33.0 mm, females 28.8–32.8 mm SUL) with moderately long limbs (TV/SUL 0.35±0.02 [0.33–0.39]), narrow snout (EN/IN 1.35±0.08 [1.24–1.60]), absence of maxillary teeth, extensively exposed frontoparietal fontanelle, faintly tubercular skin on dorsum, brown dorsal surface with paravertebral series of usually interconnected dark blotches, snout often pale gray, wide 'V' behind eyes directed posteriorly and usually bisected by vertebral row of pale tubercles, reddish-orange femoral patches, well-developed parotoid, inguinal, and coccygeal glands; inguinal gland large, rounded, and usually distinct from parotoid gland. Toes extensively webbed to second proximal tubercle on fourth toe (Fig. 2d), broadly fringed, and large thin inner and outer metatarsal tubercles.

Description. Moderate body size, squat, and rotund. Head is small with slightly protruding eyes. When viewed laterally, slightly sloping snout and slightly rounded tip; when viewed from above, the sides of the snout gradually come to a broadly rounded point. Canthus rostralis straight and poorly defined; loreal region sloping and slightly convex. Sharply pointed medial projection (synthesis of mentomeckelian bones) that matches notch on upper jaw. Nostrils directed upwards; nares with a slight rim. Anterior corner of eye covered by flap of skin; at dorsal terminus

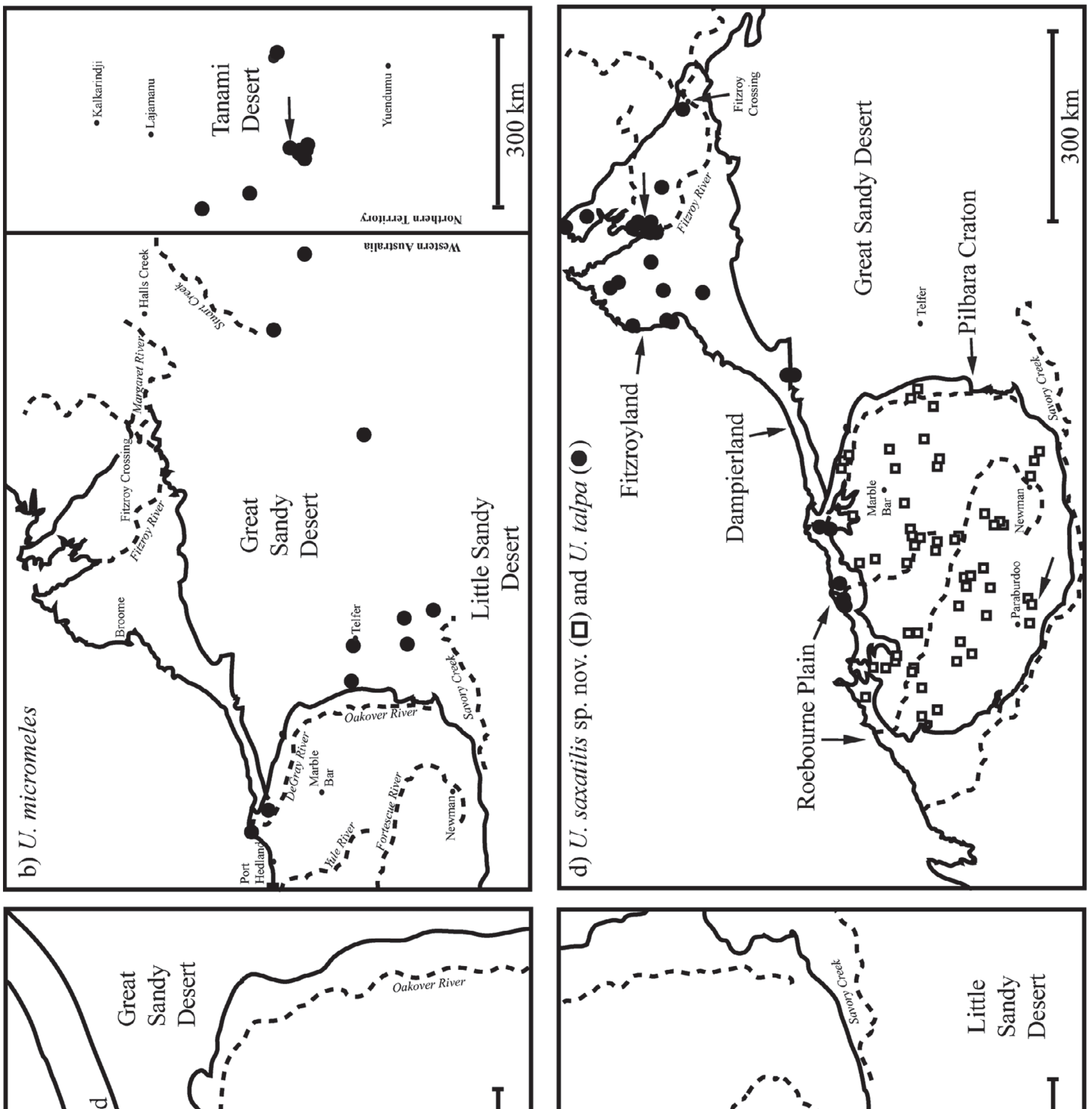

FIGURE 8. Distribution of a) *U. glandulosa*, b) *U. micromeles*, c) *U. russelli*, d) *U. saxatilis* **sp. nov.** (□) and *U. talpa* (●). Holotype locations are indicated by an arrow.

the skin overlaps the skin of the brow above the eye. Posterior edge of brow projects slightly over skin on side of head. Tympana covered by skin and parotoid glands. Tongue oval and elongate. Maxillary and vomerine teeth absent. Frontoparietal fontanelle extensively exposed. EN larger than IN (EN/IN 1.35±0.08 [1.24–1.60]).

Arms and hands thickly built. Arms are of moderate length (ArmL/SUL 0.42±0.03 [0.39–0.47]) and the fingers are poorly fringed and unwebbed. Finger length 3>4>2>1. Tubercles under fingers extensively developed; one on first and second, two on third and fourth. Palmar tubercles large, prominent and conical. Moderately developed outer palmar tubercle on distal portion of wrist. Nuptial pad of males on inner portion of first finger (beginning 1/3 down finger), extending to base of wrist (¼ along forearm) and slightly encroaching on palmar surface.

Legs moderately long (TL/SUL 0.35±0.02 [0.33–0.39]), and of moderate build. Toe length 4>3>5>2>1. Tubercles under toes moderately developed; one on first and second, two on third and fifth, three on fourth. Toes moderately long, extensively webbed to second tubercle, and strongly fringed (Fig. 2d). Poorly developed webbing between the fourth and fifth toes, reaching first tubercle on fifth toe. Large spatulate inner metatarsal tubercle, oriented along fifth toe. Outer metatarsal tubercle thin, spatulate, and oriented perpendicular to foot.

Dorsal and ventral surface slightly granular. Well developed parotoid, inguinal and coccygeal glands; inguinal rounded and rarely extends to parotoid gland. Mandibular gland well developed, discrete from parotid gland but disrupted into at least two sections.

Coloration. Dorsal ground color pale brownish-gray with wide dark brown paravertebral blotches or stripes (if connected) from anterior end of parotoid gland to coccygeal gland. Snout usually pale gray or orange, bordered behind by a wide dark brown 'V' between the eyes directed posteriorly, often extending to above eyes and disrupted in the center by vertebral row of orange tubercles; canthus rostralis often dark. Dorsolaterally along glands a wide broken pale orange-red stripe from nares extending to cloaca (Fig. 7). Lateral surfaces and upper surfaces of limbs with finer spotting, often forming thin irregular blotches; glands and upper surfaces of limbs with an orange wash. Femoral patches red or a reddish-orange when present; groin lacks flash coloration. Ventral surface translucent between finely granular whitish and gray tubercles. Large white tubercles at base of arm; inner portion of thighs translucent and entirely without pigment. Throat of males suffused with gray.

Advertisement call. Figure 6b and 6c and Table 5 summarize the main features of the call. This species has been recorded producing two calls; a long squelch of 22–38 pulses, and a short squelch of 17–26 pulses. The long call is much more common on nights of high calling activity.

Habitat. Specimens have been collected from under tufts of grass or leaf litter near the edges of creeks and rivers, alluvial flats, and along the lower pebble-strewn slopes of rocky ranges. Appears to prefer flowing rivers and streams versus the ephemeral pools of other arid zone *Uperoleia*.

Distribution. This species is restricted to the Carnarvon and Gascoyne Regions of Western Australia (Fig. 8b).

Etymology. Named for the property owner in the 1920s where the first specimens were collected, A.R.E. Russell.

Comparisons with other species. Distinguished from all western arid zone species except *U. saxatilis* **sp. nov.** by extensive toe webbing, which extends to the second proximal tubercle (Fig. 2d). *Uperoleia russelli* can be further distinguished from other western arid zone *Uperoleia* by the presence of wide dark paravertebral blotches or stripes which are absent in *U. micromeles, U. saxatilis* **sp. nov.**, and *U. talpa*. The paravertebral coloration in *U. glandulosa* is narrower and restricted to the anterior end of the dorsum.

Remarks. These data present a significant reduction in the described range of *U. russelli* and illustrates a real lack of knowledge about this species. Prior data on *U. russelli* indicated an extensive distribution across a huge area. However, over 70% of museum records of *U. russelli* actually apply to other *Uperoleia* within the arid zone and *U. russelli* has only been accurately reported from 11 different localities. Environmental assessments using previous survey work must carefully evaluate historical records for accurate species identification.

Uperoleia talpa Tyler, Davies, and Martin, 1981

Mole Toadlet

Glauertia mjobergii, Barker and Grigg, 1977, p. 199
Uperoleia talpa Tyler, Davies, and Martin, 1981 Aust. J. Zool., Suppl. Ser. 79, 1–64

Holotype. WAM R62472, collected 24 km south of Derby (17º37'S, 123º36'E), Western Australia, on 13 February 1979 by M. Davies, A.A. Martin, and M.J. Tyler.

Paratypes. There are two paratypes, an adult female SAMA R17174 and an adult male WAM R62473: collected 24–41 km south of Derby, Western Australia, on 13 February 1979 by M. Davies, A.A. Martin, and M.J. Tyler.

Diagnosis. Distinguished from congeners by a combination of large body size (males 23.7–36.1 mm, females 24.2–40.8 mm SUL) with short limbs (TL/SUL 0.33± 0.02 [0.29–0.38]), narrow squarish snout (EN/IN 1.32±0.13 [1.09–1.66]), absence of maxillary teeth, extensively exposed frontoparietal fontanelle, bronze skin with darker markings that have a centered bright red tubercle, pale salmon or non-existent femoral patches, very large hypertrophied parotoid glands that extend posterior to arms, moderately-developed inguinal and coccygeal glands which are restricted to the rear portion of the body, skin flap at anterior portion of eye palely pigmented. Toes webbed to between first and second proximal tubercle on fourth toe, and broadly oval and exceptionally large inner and outer metatarsal tubercles. A high-pitched squelch as an advertisement call.

Description. Very large body size in relation to other *Uperoleia*, squat, thick, and rotund. Head is small, thick in depth with slightly protruding eyes. When viewed laterally, slightly sloping snout and flattened tip; when viewed from above, the sides of the snout slope in strongly and terminate in a short square tip. Canthus rostralis reasonably well-defined with gradual rounded edge; loreal region steep and slightly convex. Large rounded medial projection (synthesis of mentomeckelian bones) that matches notch on upper jaw. Nostrils directed upwards; nares with no visible rim. Anterior corner of eye covered by flap of skin, which is usually palely pigmented; at dorsal terminus the skin overlaps the skin of the brow above the eye. Posterior edge of brow projects just to side of head. Tympana covered by skin and parotoid glands. Tongue oval and elongate. Maxillary and vomerine teeth absent. Frontoparietal fontanelle extensively exposed (Tyler *et al.* 1981). EN larger than IN (EN/IN 1.32±0.13 [1.09–1.66]).

Arms and hands thickly built. Arms are of moderate length (ArmL/SUL 0.41± 0.02 [0.37–0.45]) and the fingers are poorly fringed and unwebbed. Finger length 3>4>2>1. Tubercles under fingers moderately developed; one on first and second, two on third and fourth. Palmar tubercles slightly developed. Moderately developed outer palmar tubercle on distal portion of wrist. Nuptial pad of males on inner portion of first finger (beginning halfway down finger), extending to base of wrist (¼ along forearm) and slightly encroaching on palmar surface.

Legs short limbs (TL/SUL 0.33± 0.02 [0.29–0.38]) and of thick build. Toe length 4>3>5>2>1. Tubercles under toes moderately developed and conical; one on first and second, two on third and fifth, three on fourth. Toes moderately long, webbed to between first and second proximal tubercle, and moderately to strongly fringed. Webbing highly reduced between fourth and fifth toes. Large rounded inner metatarsal tubercle, slightly oriented along fifth toe. Outer metatarsal tubercle oval and oriented perpendicular to foot.

Smooth skin scattered with large tubercles on dorsum, with a raised mid-vertebral stripe. Ventral surface slightly granular. Cloacal flap present, moderately fimbriated in males and strongly fimbriated in large females. Parotoid gland extensively developed, starting from just behind eye and extending up 1/3 of body length; inguinal and coccygeal glands moderately developed and restricted to rear portion of body. Mandibular gland poorly developed, extensively disrupted when visible.

Coloration. Dorsal ground color is a dark bronze. Light brown patches are scattered across the ventral surface, frequently topped by an orange or red tubercle. Red tubercles are scattered across the ventral surface. Red tubercles form a dorso-lateral stripe extending from the snout frequently to the cloaca. Glands are pigmented in shades of red varying from light pink to crimson (Fig. 7). Femoral coloration, when present, is not extensive and appears in life as a subtle salmon wash. Ventral surface a pale off-white. Background pigment usually absent on upper inner thigh, with scattered white tubercles. Males have a darkly pigmented chin.

Advertisement call. Figure 6d and 6e summarize the two calls recorded by individuals of *U. talpa* and Table 5 summarizes the call characteristics. The first call is a short squelch formed by 27–28 pulses, where up to 1/3 of the call duration is a low amplitude 'tail'. The second call of *U. talpa* is a long squelch formed by 29–40 pulses. The long squelch is more common on nights of high calling activity.

Habitat. In the Kimberley, specimens have been collected from a variety of roadside ponds or swamps, with a mixture of *Pandanus*, *Melaleuca*, *Acacia*, and *Eucalyptus* vegetation. Specimens from near Port Hedland in the Pilbara have been collected from sandridges and red sandy loams; one was excavated from 8 cm under a Spinifex clump. As a microhabitat preference, *U. talpa* individuals prefer to be a sole occupant of an isolated grass clump or pile of leaf litter, with discrete spacing between individuals.

Distribution. *Uperoleia talpa* occurs in the Fitzroy River region near Broome and Derby, with recent records extending east as far as Fitzroy Crossing. They are further distributed south along Dampierland, a grassland between the Indian Ocean and the Great Sandy Desert, and in the eastern Roebourne Plain of the Pilbara region (Fig. 8d).

Etymology. The Latin word *talpa* (mole) refers to this species' exceptionally large metatarsal tubercles and its efficiency as a burrower.

Comparisons with other species. In the western Kimberley, *U. talpa* is distinguishable from most other congeners by its large body size (23.7–40.8 mm SUL *versus* 19–25 mm in *U. mjobergii* (Tyler & Doughty 2009), robust habitus with narrow snout, moderate webbing between the toes, dark background color with only small dark red-tipped spots, large parotoid glands, and lack of glands on the sides; its call is a short high-pitched squelch which differs from other species with clicks (*U. aspera*) or longer-duration rasps (*U. mjobergii*) as calls.

In the eastern Roebourne Plain of the Pilbara region, it differs from *U. glandulosa* by larger body size (23.7–40.8 mm SUL *versus* 20.6–27.5 mm), highly reduced inguinal glands, and a longer squelch (*versus* a sharp click) as an advertisement call; from *U. micromeles* by a narrow snout (EN/IN 1.17–1.61 *versus* 0.70–0.88), more extensive toe webbing, and darker background coloration (*versus* light brown); and from *U. russelli* by larger body size (23.7–40.8 mm SUL *versus* 20.9–33.0 mm) and small lighter brown dorsal spots (*versus* wide paravertebral blotches). It differs from the closely related *U. saxatilis* **sp. nov.** by a combination of characters including larger body size (23.7–40.8 mm SUL *versus* 24.0–36.6 mm), larger parotoid glands, and less webbing between toes (webbed to first proximal tubercle or to between first and second proximal tubercles *versus* to between first and second proximal tubercles or to the second proximal tubercle). Dorsal coloration is very distinguishing, as *U. talpa* bronze with a few light brown patches frequently topped by reddish tubercles, and *U. saxatilis* **sp. nov.** is a darker brown with numerous irregular dark brown blotches and no red tubercles. Calls between *U. talpa* and *U. saxatilis* **sp. nov.** are highly divergent. Each species produces two calls with no overlap of call characters (Table 5). The two calls of *U. talpa* have a high number of pulses when compared to *U. saxatilis* **sp. nov.** and this species does not have a long duration call (8.8 ms with 27–28 pulses per call and 12.6 ms with 33.5 pulses per call *versus* 21.6 ms with 21.3 pulses per call and 7.9 ms with 16.7 pulses per call).

Remarks. Tyler *et al.* (1981) only distinguished *U. talpa* from *U. orientalis* based on *U. talpa* being a stouter species with shorter fingers, having uniform coloration, and lacking the mid-vertebral stripe. However, the *U. orientalis* holotype was examined at the time of the *U. talpa* description, and M.J. Tyler has confirmed they are morphologically distinct (pers. comm.). Davies & Martin (1988) redescribed *U. talpa* based on a larger series of specimens, including a detailed description of the internal morphology.

Uperoleia saxatilis sp. nov.

Pilbara Toadlet

Holotype. WAMR162877, a calling male collected at Turee Creek (23º20'37.6"S, 118º1'16.6"E), Western Australia, in May 2006 by P. Doughty, C. Stevenson, and P.G. Kendrick (Fig. 9).

Paratypes. There are 10 paratypes, 4 adult males and 6 adult females: WAM R110883, a gravid female collected 36.8 km SSE of Pannawonica (21º56'28.7"S, 116º27'14.0"E), Western Australia, on 16 March 2005 by R.J. Teale; WAM R135086, a gravid female collected at Hamersley Gorge, Karijini National Park (22º15'S, 118º0'E), Western Australia, on 28 August 1996 by S.J. Reynolds; WAM R135639, a female collected at Pinga Creek Crossing (21º28'59.9"S, 118º39'0.0"E), Western Australia, on 16 February 1999 by B. Maryan and J. Smith; WAM R140012, a male collected at Millstream Chichester National Park (21º10'52.7"S, 117º3'28.1"E), Western Australia, on 12 September 1999 by Ecologia; WAM R145561, a gravid female collected 80 km S of Port Hedland (21º0'36.0"S, 118º42'0.0"E), Western Australia, on 3 May 2001 by R.J. Teale; WAM R154550, a gravid female collected at Wheelarra Hill (23º23'21.8"S, 120º9'41.0"E), Western Australia, on 12 February 2004 by M. Ladyman; WAM R154764, a male collected at Brockman Ridge (23º19'9.8"S, 119º57'11.9"E), Western Australia, on 5 April 2004 by J. Fraser; WAM R156614, a male collected at the Woodie Woodie Minesite (21º38'58.9"S, 121º14'17.2"E), Western Australia, on 11 June 2005 by M. Peterson; WAM R156222, a gravid female collected at Cattle Gorge (20º36'11.9"S, 120º15'51.1"E), Western Australia, on 17 December 2004 by M. Ladyman; and WAM R166206, a male collected 10 km S of Nullagine (21º57'16.9"S, 120º7'35.04"E) Western Australia, on 11 September 2006 by M. Peterson and K. George.

Diagnosis. Distinguished from all other *Uperoleia* by a combination of large body size (males 20.9–33.0 mm, females 27.4–36.6 mm SUL) with short limbs (TL/SUL 0.35±0.02 [0.31–0.39]), narrow snout (EN/IN 1.40±0.12 [1.18–1.66]), absence of maxillary teeth, extensively exposed frontoparietal fontanelle, brown skin with darker markings, red femoral patches when present, moderately large hypertrophied parotoid glands, moderately developed inguinal and coccygeal glands which are restricted to the rear portion of the body. Toes extensively webbed to

second proximal tubercle, and elongate, thin, and large inner and outer metatarsal tubercles. A low-pitched squelch as an advertisement call.

FIGURE 9. Photos in life (dorsolateral and dorsal views) and after preservation (ventral view) of *U. saxatilis* **sp. nov.** holotype (WAM R162877) from Turee Creek, Western Australia. Photos by P. Doughty.

Description. Moderately large body size, squat, thick and rotund. Head is small, thin in depth with slightly protruding eyes. When viewed laterally, slightly sloping snout and slightly rounded tip; when viewed from above, the sides of the snout slope in strongly and come to a short slightly rounded tip. Canthus rostralis moderately defined with gradually rounded edge; loreal region sloping and slightly convex. Moderate rounded medial projection (synthesis of mentomeckelian bones) that matches notch on upper jaw. Nostrils directed upwards; nares with slight rim. Anterior corner of eye covered by flap of skin, which is usually darkly pigmented; at dorsal terminus the skin overlaps the skin of the brow above the eye. Posterior edge of brow does not project over side of head side of head. Tympana covered by skin and parotoid glands. Tongue oval and elongate. Maxillary and vomerine teeth absent. Frontoparietal fontanelle extensively exposed. EN larger than IN (EN/IN 1.40±0.12 [1.18–1.66]).

Arms and hands thickly built. Arms are short (ArmL/SUL 0.39±0.09 [0.34–0.37]) and the fingers are poorly fringed and unwebbed. Finger length 3>4>2>1. Tubercles under fingers moderately developed; one on first and second, two on third and fourth. Palmar tubercles moderately developed. Moderately developed outer palmar tubercle on distal portion of wrist. Nuptial pad of males on inner portion of first finger (beginning halfway down finger), extending to base of wrist (¼ along forearm) and slightly encroaching on palmar surface.

Legs moderately short (TL/SUL 0.35±0.02 [0.31–0.39]) and of thick build. Toe length 4>3>5>2>1. Tubercles under toes moderately developed and conical; one on first and second, two on third and fifth, three on fourth. Toes moderately long, webbed almost to second proximal tubercle on fourth toe, and moderately to strongly fringed. Webbing highly reduced between fourth and fifth toes. Large, slightly spatulate inner metatarsal tubercle, oriented along fifth toe. Outer metatarsal tubercle spatulate and oriented perpendicular to foot.

Skin rough with large scattered tubercles on dorsum, with a raised mid-vertebral stripe. Ventral surface slightly granular. Cloacal flap present, moderately fimbriated in males and strongly fimbriated in large females. Parotoid gland extensively developed, starting from just behind eye and extending up 1/3 of body length; inguinal and coccygeal glands moderately developed and restricted to rear portion of body. Scattered glandular tubercles between inguinal and parotoid glands. Mandibular gland moderately developed and disrupted.

Coloration. Dorsal ground color is a dark brown. Blackish patches cover the dorsal surface. Red tubercles often forming a dorsolateral stripe extending from the snout to approximately between the middle of the parotoid glands. Reddish tubercles may be present on sides and upper limbs. Glands are pigmented in shades of red varying from light pink to crimson (Figs. 7 & 9). Reddish femoral coloration when present, although frequently absent. Ventral surface a pale off-white. Background pigment usually absent on upper inner thigh, with scattered white tubercles. Males have a darkly pigmented chin.

Holotype measurements. (in mm) SUL–30.1, ArmL–12.6, TL–10.7, FL–18.1, IO–4.6, EyeL–2.8, EN–2.4, IN–1.53.

Advertisement call. Figure 6f and 6g and Table 5 summarize the main features of the call. The holotype was recorded producing two calls; a long squelch of 19–24 pulses, and a short squelch of 15–19 pulses. The long call is much more common on nights of high calling activity.

Habitat. Specimens have been collected while calling from the banks of rocky creeks.

Distribution. Extensive sampling has shown this species to be restricted to the rocky Pilbara Craton. Apparently adapted to rocky landscapes, this species does not occur in any of the sandy regions surrounding the Pilbara, including the Roebourne Plain (Fig. 8d).

Etymology. The Latin word *saxatilis* is an adjective meaning 'associated with rocks' referring to the distribution of this species on the rocky Pilbara craton.

Comparisons with other species. This species can be distinguished from *U. glandulosa* and *U. russelli* by absence of red to golden glands connecting along the sides, possessing a darker ground coloration and many small dark dorsal blotches (*versus* larger, often interconnecting blotches). In addition, *U. saxatilis* differs from the sympatric *U. glandulosa* by having more extensive webbing between the toes (to between first and second or to second proximal tubercle *versus* to first proximal tubercle) and a squelch (*versus* a click) as an advertisement call. Near the edges of the Pilbara craton *U. micromeles* may also closely occur; from this species *U. saxatilis* can be distinguished by narrower snout (EN/IN 1.18–1.58 *versus* 0.70–0.88), more extensive webbing (to between first and second or to second proximal tubercle *versus* basal) and lacking fine white tubercles on sides of snout and above eyes. *Uperoleia saxatilis* is most similar morphologically to its sister species *U. talpa* and is compared extensively in the *U. talpa* description above.

Discussion

Broader Phylogeny of *Uperoleia*. We provide the first estimate of phylogenetic relationships within the myobatrachid frog genus *Uperoleia*. Comprehensive mtDNA screening of our target species and our multi-locus data set each provide strong evidence for four major species-rich clades within *Uperoleia*. The results of this study reveal that there are not two (*U. russelli, U. glandulosa*) but rather five divergent evolutionary lineages in the Pilbara and surrounding arid regions.

Three of the four *Uperoleia* clades recovered from our analysis have large regions of sympatry across Australia. Species in clade 1 inhabit all of northern Australia, from *U. glandulosa* on the Roebourne Plain and in the Yule River, *U. lithomoda*, *U. trachyderma*, *U. aspera*, *U. minima*, *U. altissima*, and *U. littlejohni* across regions of monsoonal northern Australia (Kimberley, Top End, and Cape York), and *U. rugosa* in the more arid inland east coast (Barker *et al*. 1995; Cogger 2000). Clade 2 species are located in the Fitzroyland and Kimberley regions (Cogger 2000) where they co-occur with species in clades 1 and 3. *Uperoleia micromeles*, a member of clade 2, is largely allopatric to all other *Uperoleia* in the desert regions of Australia, although its distribution overlaps slightly with *U. glandulosa* and *U. talpa* at the western edges of the Great Sandy Desert and the Roebourne Plain of the coastal Pilbara (Fig. 8b). Species in clade 3 are distributed in the Kimberley and Fitzroyland regions (Cogger 2000) where they are sympatric with species in clades 1 and 2. Clade 3 also has two allopatric species in the western arid zone (*U. saxatilis* in the Pilbara, *U. russelli* in the Carnarvon and Gascoyne Regions). The three sympatric species in clade 4 are most divergent from the rest of *Uperoleia*. The species in this clade are allopatric with other clades of *Uperoleia* and are restricted to east of the Great Dividing Range on the east coast of Australia (Cogger 2000; R. Catullo unpublished data).

Our phylogeny adds to the data suggesting that monophyly of arid and mesic taxa cannot be assumed *a priori* within a phylogeny, as we have evidence for at least three divergences between western arid zone and monsoonal tropics taxa. Previous evidence has been conflicting, either showing that taxa that inhabit the arid zone are mono-

phyletic as in skinks (Rabosky *et al.* 2007) and eucalypts (Ladiges *et al.* 2010), or that there have been multiple divergences between arid and mesic taxa as in geckos (Fujita *et al.* 2010) or birds (Toon *et al.* 2010). The role that organismal ecology and biogeographic history play in the different evolutionary histories of these taxa is still largely unexplored.

The corrected genetic distance for mitochondrial gene ND2 between *U. talpa* and *U. saxatilis* is extremely small (1.7%, Table 2b), likely indicating the speciation is relatively recent. The only Myobatrachid species pair known to show a lower value of interspecific genetic divergence (0.8% in ND2) are *Geocrinia laevis* and *G. victoriana* (Read *et al.* 2001). However, as in this case, the divergences between *Geocrinia* species are supported by morphology and advertisement call data (Gartside *et al.* 1979).

Biogeography of western arid zone *Uperoleia*. *Uperoleia glandulosa* appears to be restricted to boundaries that strongly correlate with geology, as it is present only within the sandy eastern Roebourne Plain and inland along the Yule River in the northern Pilbara. The absence of *U. glandulosa* in the western Roebourne Plain may be due to the extension of the Chichester Range to the coast (Fig. 1), blocking expansion further along the plain or may be an artifact of poor sampling on the western Roebourne Plain. *Uperoleia micromeles* is found within the extreme arid zone deserts, which are characterized by extensive dunefields made primarily of red siliceous sand (Beard & Webb 1974). Although it occurs on the periphery of the Pilbara craton on the eastern and northern boundaries, this species has not been found outside of the sand dunes or along the Dampierland grasslands that connect the Fitzroyland region with the Pilbara. *Uperoleia russelli* was previously believed to be present on the Roebourne Plain, the rocky Pilbara craton, and in the Carnarvon and Gascoyne regions to the south of the Pilbara (Tyler *et al.* 1981; Cogger 2000). However, our results show *U. russelli* is a divergent species that is restricted to the Carnarvon and Gascoyne regions, which are characterized by red iron-rich soil and coastally by sandy calcareous soils (Beard 1975). We speculate that this species may be a sandy soil specialist and therefore restricted by the sedimentary rocks of the Hamersley Ranges (Van Kranendonk *et al.* 2002). These ranges may prevent dispersal into the Pilbara craton to the northeast. Expansion into the Little Sandy Desert in the southeast may be restricted by a combination of the granitic rocks of the Gascoyne Complex (Beard & Webb 1974; Beard1975) and increasing aridity.

The sharp boundary at the eastern edge of the Pilbara craton that we see in the *U. saxatilis* distribution has been shown to be important in the distributional limits of sand and rock dwelling clades of the gecko *Lucasium (Diplodactylus) stenodactylum* (Pepper *et al.* 2006). Pepper *et al.* (2006) found this to be a distinct boundary between *L. stenodactylum* on the Pilbara craton and the monophyletic genetic group in the Great Sandy Desert. However, they did not find the dramatic change in species distributions at all major geological boundaries, such as between the Pilbara craton and the Roebourne Plain, or between the Pilbara craton and the Carnarvon and Gascoyne Regions, as we have found here. *Uperoleia saxatilis* is probably restricted to rocky regions.

The wide distribution of *U. talpa* across the sandy areas of Fitzroyland in the Monsoonal Tropics into Dampierland and the Roebourne Plain in the arid zone may indicate a stronger tolerance to severe conditions than many other *Uperoleia.* It is a larger burrowing species, a characteristic is shares with the *Cyclorana australis* and *C. longipes* that also inhabit the Fitzroyland region and cross Dampierland into the Pilbara region (Tyler & Doughty 2009). *Uperoleia talpa* is not found north in the Kimberley, probably due to the King Leopold Range. Extensive sampling in the Pilbara shows that *U. talpa* is only present on the sandy soils the Roebourne Plain and not further inland on the rocky Pilbara craton (Hickman 1993). Further studies using molecular dating will allow better testing of the influence of substrate, geology, and climate on speciation.

Taxonomic implications. Based on our detailed phylogenetic and morphological data sets, we above describe the clade restricted to the rocky Pilbara craton as a new species, *Uperoleia saxatilis*. This clade is very well supported by our molecular data, which includes fixed differences at multiple nuclear loci. The molecular data, in combination with the parapatric distribution of the clades, demonstrates probable reproductive isolation between *U. talpa* and *U. saxatilis*. Our morphometric data show that this new taxon and its sister species, *U. talpa,* overlap in body proportions (Fig. 5) but *U. saxatilis* are distinguishable from *U. talpa* using a number of morphological features (see descriptions above) as well as distinctive call differences. Species status of the other four taxa found in the western arid zone (*U. glandulosa, U. micromeles, U. russelli,* and *U. talpa*) is strongly supported by both genetic and morphological data.

The description of *U. saxatilis* brings the total number of *Uperoleia* species up to 27, making it by far the largest genus of myobatrachid frogs. This study underscores the potential for more cryptic species to exist within currently recognized *Uperoleia* species owing to their conservative morphology and often remote distributions.

Acknowledgements

We thank the South Australian Museum for providing tissue samples and access to vouchers, the Herman Slade Foundation for funding of genetic sequencing, the Environmental Futures Network for funding travel for morphological training, Department of Environment and Conservation (WA) and Alcoa Frog Watch for support in the field, Erin Walsh for the foot drawings and assistance with figures, Marion Anstis and Henry Cook for photographs, Conrad Hoskin and Michael J. Tyler for comments on the manuscript, Mitzy Pepper for helpful discussions on western arid zone geology and Simon Ho of University of New South Wales and David Moore for assistance in molecular analysis.

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APPENDIX 1. Details of specimens included and data generated in this study. The column 'Museum ID' shows the museum and registration number as follows: Western Australian Musuem (WAM), South Australian Museum (SAMA), Queensland Museum (QM), Northern Territory Museum (NTM), and Northern Territory Faunal Survey Records (NTFS). The 'Lab ID' column refers to our internal codes for tissue samples and we use these numbers in the phylograms. The 'Data' column indicates whether a specimen was sequenced for mtDNA genes 16S and ND2 (mt), nDNA genes RAG1, POMC, and BNDF (n), included in morphological analysis (M), for vouchers sorted by morphology for additional distributional data (D), and (E) for field survey records. The Latitude and Longitude are in Decimal Degrees.

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
Spicospina flammocaerulea	SAMAABTC69165	Myo121	mt, n	-34.76667	116.96667	24–30 km NE of Walpole, WA
U. altissima	QM N75766	Up0400	mt, n	-17.63694	145.45910	Millstream National Park, NE QLD
U. aspera	WAM R164676	Up0245	mt, n	-17.8280	124.2653	65km E of junction between Great Northern Hwy and Derby Rd, WA
U. borealis	WAM R162484	Up0162	mt, n	-15.86840	128.92835	24 km E of Kununurra, WA
U. crassa	WAM R167727	Up0193	mt, n	-14.82020	125.72110	Mitchell Plateau, WA
U. fusca	this study	Up0056	mt, n	-28.59110	153.38160	Whian Whian, NSW
U. glandulosa	WAM R22921		M	-20.5166	118.1000	5 km E of Mundabullangana, WA
U. glandulosa	WAM R89489		D	-20.3833	118.8000	Petermarer Creek, WA
U. glandulosa	WAM R89490		M	-20.3833	118.8000	Petermarer Creek, WA
U. glandulosa	WAM R89491		M	-20.3833	118.8000	Petermarer Creek, WA
U. glandulosa	WAM R89492		M	-20.3833	118.8000	Petermarer Creek, WA
U. glandulosa	WAM R89493		M	-20.4166	118.7000	7 km NNE of Pippengarra Homestead, WA
U. glandulosa	WAM R90738		D	-21.6677	119.0408	200m S of Gallery Hill, WA
U. glandulosa	WAM R90739		D	-21.6677	119.0408	200m S of Gallery Hill, WA
U. glandulosa	WAM R90744		D	-21.6166	118.9500	200 m W of Woodstock Homestead, WA
U. glandulosa	WAM R90745		M	-21.6166	118.9500	200 m W of Woodstock Homestead, WA
U. glandulosa	WAM R90774		M	-21.6166	118.9500	200 m W of Woodstock Homestead, WA
U. glandulosa	WAM R99924		D	-21.6166	119.0233	Woodstock Station, WA
U. glandulosa	WAM R99944		D	-21.6116	118.9556	Woodstock Station, WA
U. glandulosa	WAM R99961		D	-21.6111	119.0397	Woodstock Station, WA
U. glandulosa	WAM R100596		M	-21.6169	118.9536	Woodstock Station, WA
U. glandulosa	WAM R100597		M	-21.6169	118.9536	Woodstock Station, WA
U. glandulosa	WAM R115638	Up0085	mt, n, M	-20.33330	119.21670	Strelly River, WA
U. glandulosa	WAM R115639	Up0086	mt, M	-20.33330	119.21670	Strelly River, WA
U. glandulosa	WAM R135637	Up0095	mt	-21.48330	118.65000	Pinga Creek Crossing, WA
U. glandulosa	WAM R135895		M	-20.7666	118.4167	40 km SSW of South Hedland, WA
U. glandulosa	WAM R135900	Up0102	mt, n, M	-20.31660	119.20000	Strelley River Crossing, WA
U. glandulosa	WAM R135901	Up0103	mt, M	-20.31660	119.20000	Strelley River Crossing, WA

......*continued on next page*

APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. glandulosa	WAM R154273	Up0129	mt, n, M	-21.91330	118.97170	Fortescue Marsh, WA
U. glandulosa	WAM R161230		M	-20.5256	118.077	45 km NNE of Whim Creek Hotel, WA
U. glandulosa	WAM R161231		D	-20.5256	118.077	45 km NNE of Whim Creek Hotel, WA
U. glandulosa	WAM R161233		M	-20.5256	118.077	45 km NNE of Whim Creek Hotel, WA
U. glandulosa	WAM R161264		D	-20.5256	118.077	45 km NNE of Whim Creek Hotel, WA
U. glandulosa	WAM R163776		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163777		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163794		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163795		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163802		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163803		M	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163806		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163807		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163809		M	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163814		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163815		M	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163816		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163817		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R163818		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. glandulosa	WAM R166488	Up0152	mt, M	-20.25110	119.16080	60 km E of Port Hedland, WA
U. glandulosa	WAM R166492		M	-20.2511	119.1608	60 km E of Port Hedland, WA
U. inundata	NTM R35103	Up0270	mt, n	-12.55750	131.29633	Fogg Dam, NT
U. laevigata	this study	Up0040	mt, n	-30.45640	150.20920	Ebor Quarry, NSW
U. lithomoda	WAM R162466	Up0157	mt, n	-15.77490	128.67957	10 km W of Kununurra, WA
U. littlejohni	this study	Up0394	mt, n	-17.34222	145.41750	Mt. Baldy, QLD
U. micra	WAM R168039	Up0220	mt, n	-15.99050	125.33060	Prince Regent River Nature Reserve, WA
U. micromeles	NTFS 134757		E	-20.86600	130.41000	Tanami Desert, NT
U. micromeles	NTFS 134785		E	-20.87800	128.65800	Tanami Desert, WA
U. micromeles	NTFS 135160		E	-20.88330	130.40000	Tanami Desert, NT
U. micromeles	NTFS 135304		E	-20.83330	130.40000	Tanami Desert, NT
U. micromeles	NTFS 135346		E	-20.36670	131.91670	Tanami Desert, NT
U. micromeles	NTFS 135542		E	-20.63330	130.41670	Tanami Desert, NT
U. micromeles	NTFS 135828		E	-20.86800	130.41300	Tanami Desert, NT
U. micromeles	NTFS 136347		E	-20.86800	130.41300	Tanami Desert, NT
U. micromeles	NTFS 136415		E	-20.86800	130.41300	Tanami Desert, NT
U. micromeles	NTFS 136442		E	-20.41600	131.97700	Tanami Desert, NT
U. micromeles	NTFS 136721		E	-20.88330	130.40000	Tanami Desert, NT
U. micromeles	NTFS 136806		E	-20.36670	131.90000	Tanami Desert, NT
U. micromeles	NTFS 136955		E	-20.78330	130.33330	Tanami Desert, NT
U. micromeles	NTFS 136966		E	-20.86670	130.26670	Tanami Desert, NT
U. micromeles	NTFS 137202		E	-20.88330	130.40000	Tanami Desert, NT
U. micromeles	NTFS 137357		E	-19.18180	129.40920	Tanami Desert, NT
U. micromeles	NTFS 137507		E	-20.88330	130.41670	Tanami Desert, NT
U. micromeles	NTFS 137820		E	-20.41300	131.96900	Tanami Desert, NT
U. micromeles	NTFS 137961		E	-20.36670	131.91670	Tanami Desert, NT
U. micromeles	NTFS 137962		E	-20.36670	131.91670	Tanami Desert, NT
U. micromeles	NTFS 138019		E	-19.97000	129.67000	Tanami Desert, NT
U. micromeles	NTFS 138078		E	-20.36670	131.91670	Tanami Desert, NT
U. micromeles	NTFS 138134		E	-19.97000	129.67000	Tanami Desert, NT
U. micromeles	NTFS 138270		E	-20.91670	130.45000	Tanami Desert, NT
U. micromeles	NTFS 138647		E	-20.87200	130.41200	Tanami Desert, NT
U. micromeles	NTFS 138848		E	-20.86300	130.41200	Tanami Desert, NT
U. micromeles	NTM R14769		E	-20.83330	130.40000	East of Sangsters Bore, Tanami Desert, NT
U. micromeles	NTM R15907		E	-20.36660	131.91660	Lander River Floodout, Tanami Desert, NT

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. micromeles	NTM R15908		E	-20.36660	131.91660	Lander River Floodout, Tanami Desert, NT
U. micromeles	NTM R15909		E	-20.36660	131.91660	Lander River Floodout, Tanami Desert, NT
U. micromeles	NTM R18767		E	-19.18180	129.40910	Stake Range, Tanami Desert, NT
U. micromeles	NTM R18768		E	-19.18180	129.40910	Stake Range, Tanami Desert, NT
U. micromeles	NTM R18769		E	-19.18180	129.40910	Stake Range, Tanami Desert, NT
U. micromeles	NTM R20476		E	-20.86660	130.41660	500 m NW of Fiddlers Lake, NT
U. micromeles	NTM R20504		E	-20.86660	130.41660	500 m NW of Fiddlers Lake, NT
U. micromeles	NTM R30001		E	-20.88330	130.41660	Sangsters Bore, Tanami Desert, NT
U. micromeles	NTM R31197		E	-20.88330	130.40000	Salt Beef Lake, Tanami Desert, NT
U. micromeles	NTM R31198		E	-20.88330	130.40000	Salt Beef Lake, Tanami Desert, NT
U. micromeles	NTM R31199		E	-20.63330	130.41660	Tanami Desert, NT
U. micromeles	NTM R31206		E	-20.63330	130.41660	Tanami Desert, NT
U. micromeles	SAMAABTC12487	Up0790	mt	-20.63330	130.41660	Tanami Desert, NT
U. micromeles	SAMAABTC12488	Up0791	mt	-20.63330	130.41660	Tanami Desert, NT
U. micromeles	SAMAABTC12490	Up0792	mt	-20.63330	130.41660	Tanami Desert, NT
U. micromeles	SAMAABTC12491	Up0793	mt	-20.63330	130.41660	Tanami Desert, NT
U. micromeles	SAMAABTC12492	Up0795	mt	-20.63330	130.41660	Tanami Desert, NT
U. micromeles	SAMAABTC12493	Up0796	mt, n	-20.63330	130.41660	Tanami Desert, NT
U. micromeles	WAM R63815		D	-22.5333	122.6167	1 km S of Talbot Soak, WA
U. micromeles	WAM R64073		D	-20.3666	127.4000	1 km S of Staffords Bore, WA
U. micromeles	WAM R81442		D	-22.5833	122.1833	Rudall River, WA
U. micromeles	WAM R81452		D	-22.5833	122.1833	Rudall River, WA
U. micromeles	WAM R83742		D	-23.0166	122.7500	Binna-Binna Pool, MacKay Creek, WA
U. micromeles	WAM R83743		D	-23.0166	122.7500	Binna-Binna Pool, MacKay Creek, WA
U. micromeles	WAM R83744		D	-23.0166	122.7500	Binna-Binna Pool, MacKay Creek, WA
U. micromeles	WAM R83762		D	-23.0166	122.7500	Binna-Binna Pool, MacKay Creek, WA
U. micromeles	WAM R83763		D	-23.0166	122.7500	Binna-Binna Pool, MacKay Creek, WA
U. micromeles	WAM R96912		M	-21.8666	125.6667	Well 38, Canning Stock Route, WA
U. micromeles	WAM R96913		M	-21.8666	125.6667	Well 38, Canning Stock Route, WA
U. micromeles	WAM R115640	Up0087	mt, n, M	-20.00000	119.06670	50 km N. of Port Hedland, WA
U. micromeles	WAM R115641	Up0088	mt, M	-20.00000	119.06670	50 km N. of Port Hedland, WA
U. micromeles	WAM R127136		M	-21.6666	121.5833	Nifty Mine, WA
U. micromeles	WAM R127137		M	-21.6666	121.5833	Nifty Mine, WA
U. micromeles	WAM R127138		M	-21.6666	121.5833	Nifty Mine, WA
U. micromeles	WAM R127139		M	-21.6666	121.5833	Nifty Mine, WA
U. micromeles	WAM R127140		M	-21.6666	121.5833	Nifty Mine, WA
U. micromeles	WAM R137913	Up0104	mt, n, M	-21.69190	122.15890	Telfer, WA
U. micromeles	WAM R163768		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163778		M	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163792		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163793		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163796		M	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163801		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163804		M	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163805		M	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163808		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163810		M	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163811		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. micromeles	WAM R163812		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163813		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163819		M	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. micromeles	WAM R163820		D	-20.2839	119.432	12 km WNW of Goldsworthy, WA
U. minima	WAM R167878	Up0201	mt, n	-14.87020	125.82500	Mitchell Plateau, WA
U. mjobergi	WAM R164619	Up0230	mt, n	-17.4530	124.2242	62 km E Derby on Gibb River Road, WA
U. rugosa	SAMAABTC03645	Up0606	mt, n	-34.067	145.417	Gunbar, NSW
U. russelli	SAMAABTC11689	Up0745	mt	-25.050	115.200	Gascoyne Junction, WA
U. russelli	SAMAABTC11690	Up0746	mt	-25.050	115.200	Gascoyne Junction, WA
U. russelli	SAMAABTC11691	Up0747	mt, n	-25.050	115.200	Gascoyne Junction, WA
U. russelli	SAMAABTC11692	Up0748	mt	-25.050	115.200	Gascoyne Junction, WA
U. russelli	SAMAABTC11693	Up0749	mt	-25.050	115.200	Gascoyne Junction, WA
U. russelli	SAMAABTC11733	Up0750	mt	-22.900	114.950	Barradale Roadhouse, Yannarie River, WA
U. russelli	SAMAABTC11734	Up0751	mt	-22.900	114.950	Barradale Roadhouse, Yannarie River, WA
U. russelli	SAMAABTC11735	Up0752	mt	-22.900	114.950	Barradale Roadhouse, Yannarie River, WA
U. russelli	SAMAABTC11736	Up0753	mt	-22.900	114.950	Barradale Roadhouse, Yannarie River, WA
U. russelli	WAM R2368		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2608		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2609		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2610		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2611		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2612		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2613		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2614		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2615		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2616		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2617		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2618		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2619		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2620		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2621		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2622		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2623		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2624		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2625		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2626		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2627		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2628		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2629		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2630		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2631		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2632		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2633		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2634		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2635		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2636		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2637		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2638		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2639		D	-25.0000	117.0000	Aurillia Creek, Landor, WA

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. russelli	WAM R2640		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2641		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2642		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2643		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2644		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2645		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2646		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2647		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R2648		D	-25.0000	117.0000	Aurillia Creek, Landor, WA
U. russelli	WAM R10355		D	-23.8500	113.9667	Minilya, WA
U. russelli	WAM R10356		D	-23.8500	113.9667	Minilya, WA
U. russelli	WAM R10357		D	-23.8500	113.9667	Minilya, WA
U. russelli	WAM R10358		D	-23.8500	113.9667	Minilya, WA
U. russelli	WAM R10389		D	-23.8500	113.9667	Minilya, WA
U. russelli	WAM R10390		D	-23.8500	113.9667	Minilya, WA
U. russelli	WAM R10391		D	-23.8500	113.9667	Minilya, WA
U. russelli	WAM R10392		D	-23.8500	113.9667	Minilya, WA
U. russelli	WAM R112535	Up0112	mt, n, M	-24.85610	113.70330	8 Km E of Carnarvon, WA
U. russelli	WAM R112536	Up0113	mt, M	-24.85610	113.70330	8 Km E of Carnarvon, WA
U. russelli	WAM R112540	Up0114	mt, M	-24.85610	113.70330	Lewers Creek, 6 km E of Carnarvon, WA
U. russelli	WAM R112547	Up0115	mt, M	-24.81250	113.79330	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112547		D	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112548	Up0116	mt, M	-24.81250	113.79330	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112548		D	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112549		M	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112550		D	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112560	Up0118	mt, M	-24.85610	113.70330	Lewers Creek, 6 km E of Carnarvon, WA
U. russelli	WAM R112561		M	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112564		D	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112565	Up0119	mt, M	-24.85610	113.70330	Lewers Creek, 6 km E of Carnarvon, WA
U. russelli	WAM R112566		D	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112584		D	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112585	Up0120	mt, M	-24.85610	113.70330	8 Km E of Carnarvon, WA
U. russelli	WAM R112586	Up0121	mt, M	-24.85610	113.70330	8 Km E of Carnarvon, WA
U. russelli	WAM R112587	Up0122	mt, M	-24.85610	113.70330	8 Km E of Carnarvon, WA
U. russelli	WAM R112588		D	-24.8561	113.7033	8 Km E of Carnarvon, WA
U. russelli	WAM R112589		M	-24.8561	113.7033	8 Km E of Carnarvon, WA
U. russelli	WAM R112590		D	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112591		M	-24.8561	113.7033	8 Km E of Carnarvon, WA
U. russelli	WAM R112592		M	-24.8561	113.7033	8 Km E of Carnarvon, WA
U. russelli	WAM R112596		D	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R112597		D	-24.8125	113.7933	Brick House, 19 km E of Carnarvon, WA
U. russelli	WAM R117696	Up0123	mt, M	-24.86000	113.66890	5 km E of Carnarvon, WA
U. russelli	WAM R125612		D	-25.0552	115.2939	9 km E of Gascoyne Junction, WA
U. russelli	WAM R125622		D	-25.2100	115.5142	39 km ESE of Gascoyne Junction, WA
U. russelli	WAM R125624		D	-25.2100	115.5142	39 km ESE of Gascoyne Junction, WA
U. russelli	WAM R126230		M	-25.6538	114.6256	1.2 km NE of Meedo Homestead, WA
U. russelli	WAM R126231		D	-25.6538	114.6256	1.2 km NE of Meedo Homestead, WA
U. russelli	WAM R126232		D	-25.6538	114.6256	1.2 km NE of Meedo Homestead, WA
U. russelli	WAM R126233		D	-25.6538	114.6256	1.2 km NE of Meedo Homestead, WA
U. russelli	WAM R135077	Up0089	mt, n, M	-24.31660	116.80000	Mt. Augustus Summit Trail, WA
U. russelli	WAM R138090		M	-24.5166	116.9000	Thomas River Crossing, WA
U. russelli	WAM R138091	Up0105	mt, M	-24.51660	116.90000	Thomas River Crossing, WA
U. russelli	WAM R151133		D	-24.8600	113.6689	Carnarvon, WA

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. saxatilis sp. nov.	WAM R12934		D	-21.5833	117.0667	Millstream, WA
U. saxatilis sp. nov.	WAM R12935		D	-21.5833	117.0667	Millstream, WA
U. saxatilis sp. nov.	WAM R20244		D	-21.5666	117.0167	5 km W of Millstream, WA
U. saxatilis sp. nov.	WAM R20245		D	-21.6333	117.6000	Tambrey Homstead, WA
U. saxatilis sp. nov.	WAM R20246		D	-21.6333	117.6000	Tambrey Creek, WA
U. saxatilis sp. nov.	WAM R20247		D	-21.6333	117.6000	Tambrey Creek, WA
U. saxatilis sp. nov.	WAM R20248		D	-21.5833	117.0667	Millstream, WA
U. saxatilis sp. nov.	WAM R20249		D	-21.6333	117.6000	Tambrey Creek, WA
U. saxatilis sp. nov.	WAM R20250		D	-21.6333	117.6000	Tambrey Creek, WA
U. saxatilis sp. nov.	WAM R20251		D	-21.6333	117.6000	Tambrey Creek, WA
U. saxatilis sp. nov.	WAM R20252		D	-21.6333	117.6000	Tambrey Creek, WA
U. saxatilis sp. nov.	WAM R20254		D	-21.5833	117.0667	Millstream, WA
U. saxatilis sp. nov.	WAM R20255		D	-21.5833	117.0667	Millstream, WA
U. saxatilis sp. nov.	WAM R22907		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R22908		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R22909		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R22910		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R22911		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R22912		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R22913		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R22914		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R22915		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R22916		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R22917		D	-21.3166	120.0500	Mt. Edgar, WA
U. saxatilis sp. nov.	WAM R26253		D	-22.6500	119.3667	Weeli Wolli Creek, WA
U. saxatilis sp. nov.	WAM R26254		D	-22.6500	119.3667	Weeli Wolli Creek, WA
U. saxatilis sp. nov.	WAM R26255		D	-22.6500	119.3667	Weeli Wolli Creek, WA
U. saxatilis sp. nov.	WAM R33211		D	-21.6166	118.9500	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R34747		D	-21.5833	117.0667	Millstream, WA
U. saxatilis sp. nov.	WAM R39078		D	-21.8833	121.0000	Skull Springs, Davis River, WA
U. saxatilis sp. nov.	WAM R39079		D	-21.8833	121.0000	Skull Springs, Davis River, WA

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. saxatilis sp. nov.	WAM R42434		D	-22.9166	119.2167	Weeli Wooli Spring, W of Marillana, WA
U. saxatilis sp. nov.	WAM R45077		D	-21.5000	117.6000	10 km N or Tambrey
U. saxatilis sp. nov.	WAM R45668		D	-21.7500	120.5000	Mosquito Creek, WA
U. saxatilis sp. nov.	WAM R63110		D	-21.9666	120.2000	Nullagine, WA
U. saxatilis sp. nov.	WAM R63133		D	-21.5333	121.1167	Upper Carawine Pool, WA
U. saxatilis sp. nov.	WAM R63134		D	-21.5333	121.1167	Upper Carawine Pool, WA
U. saxatilis sp. nov.	WAM R68944		D	-22.2416	117.1814	Millstream, WA
U. saxatilis sp. nov.	WAM R68945		D	-22.2416	117.1814	Millstream, WA
U. saxatilis sp. nov.	WAM R73162		D	-22.7808	119.2189	Marillana Homstead, WA
U. saxatilis sp. nov.	WAM R73492		D	-21.9000	118.8333	Beabea Creek, 14 km SSE of White Springs, WA
U. saxatilis sp. nov.	WAM R73493		D	-21.9000	118.8333	Beabea Creek, 14 km SSE of White Springs, WA
U. saxatilis sp. nov.	WAM R75841		D	-22.4000	118.4500	Kalamina Gorge, WA
U. saxatilis sp. nov.	WAM R82601		D	-22.3500	118.4333	Kalamina Gorge, WA
U. saxatilis sp. nov.	WAM R83215		D	-20.9833	117.1000	41 km SE of Karratha, WA
U. saxatilis sp. nov.	WAM R90646		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R90737		D	-21.6677	119.0408	200m S of Gallery Hill, WA
U. saxatilis sp. nov.	WAM R90881		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R90917		D	-21.5347	119.1483	Cadjeput Rock Pool, WA
U. saxatilis sp. nov.	WAM R90918		D	-21.5347	119.1483	Cadjeput Rock Pool, WA
U. saxatilis sp. nov.	WAM R90920		D	-21.5347	119.1483	Cadjeput Rock Pool, WA
U. saxatilis sp. nov.	WAM R90921		D	-21.5347	119.1483	Cadjeput Rock Pool, WA
U. saxatilis sp. nov.	WAM R90922	Up0079	mt, M	-21.53470	119.14830	Cadjeput Rock Pool, WA
U. saxatilis sp. nov.	WAM R94873		D	-23.3208	117.7417	Neerambah Spring, WA
U. saxatilis sp. nov.	WAM R99329		D	-21.6116	118.9556	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99333		D	-21.6111	119.0397	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99391		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99392		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99393		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99394		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99395		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99396		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99397		D	-21.6169	118.9536	Woodstock Station, WA

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. saxatilis sp. nov.	WAM R99398		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99399		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99400		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99899		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99900		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99908		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99911		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99920		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99921		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99922		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99923		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99930		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99931		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99934		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99935		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99936		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99942		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99943		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99960		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99970		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99971		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99972		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99973		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99974		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99975		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99976		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99977		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99978		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99979		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99980		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99981		D	-21.6169	118.9536	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99985		D	-21.6166	119.0233	Woodstock Station, WA

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. saxatilis sp. nov.	WAM R99992		D	-21.6111	119.0397	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99993		D	-21.6111	119.0397	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99996		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99997		D	-21.6166	119.0233	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R99998		D	-21.6116	118.9556	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R100595		D	-21.6677	119.0408	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R100659		D	-21.5263	119.1492	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R100660	Up0081	mt	-21.52630	119.14920	Woodstock Station, Site 15, WA
U. saxatilis sp. nov.	WAM R100661	Up0082	mt	-21.52630	119.14920	Woodstock Station, Site 15, WA
U. saxatilis sp. nov.	WAM R100662		D	-21.5263	119.1492	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R102198	Up0072	mt	-21.58330	117.06670	Millstream HS, WA
U. saxatilis sp. nov.	WAM R102528		D	-21.5847	117.0689	Millstream-Chichester National Park, WA
U. saxatilis sp. nov.	WAM R102529		D	-21.5847	117.0689	Millstream-Chichester National Park, WA
U. saxatilis sp. nov.	WAM R104018		D	-21.6166	118.9533	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R104023		D	-21.6166	118.9533	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R104231		D	-21.5263	119.1492	Woodstock Station, WA
U. saxatilis sp. nov.	WAM R108351		D	-20.4863	120.0878	Sunrise Hill, WA
U. saxatilis sp. nov.	WAM R108352		D	-20.5163	120.1350	Sunrise Hill, WA
U. saxatilis sp. nov.	WAM R108355		D	-20.4802	120.0817	Sunrise Hill, WA
U. saxatilis sp. nov.	WAM R110153		D	-21.5773	117.062	2.1 km NNE of Millstream, WA
U. saxatilis sp. nov.	WAM R110177		D	-21.33	117.25	1 km N of Python Pool, WA
U. saxatilis sp. nov.	WAM R110178		D	-21.33	117.25	1 km N of Python Pool, WA
U. saxatilis sp. nov.	WAM R110179		D	-21.33	117.25	1 km N of Python Pool, WA
U. saxatilis sp. nov.	WAM R110881	Up0138	mt, M	-21.94130	116.45390	36.8 km SSE of Pannawonica, WA
U. saxatilis sp. nov.	WAM R110882	Up0139	mt, M	-21.94130	116.45390	36.8 km SSE of Pannawonica, WA
U. saxatilis sp. nov.	WAM R110883	Up0140	mt, M	-21.94130	116.45390	36.8 km SSE of Pannawonica, WA
U. saxatilis sp. nov.	WAM R111669		D	-22.37	118.29	Knox Gorge, WA
U. saxatilis sp. nov.	WAM R111670		D	-22.37	118.29	Knox Gorge, WA
U. saxatilis sp. nov.	WAM R111685		D	-22.67	117.86	7 km ENE of Tom Price, WA
U. saxatilis sp. nov.	WAM R111691		D	-22.36	118.29	Weano Gorge, WA
U. saxatilis sp. nov.	WAM R111828		D	-23.49	120.32	11 km N of Red Hill, WA
U. saxatilis sp. nov.	WAM R111829		D	-23.49	120.32	11 km N of Red Hill, WA

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. saxatilis sp. nov.	WAM R111830		D	-23.49	120.32	11 km N of Red Hill, WA
U. saxatilis sp. nov.	WAM R114440		D	-20.6666	119.3500	Shaw River, WA
U. saxatilis sp. nov.	WAM R114441		D	-20.6666	119.3500	Shaw River, WA
U. saxatilis sp. nov.	WAM R114442		D	-20.6666	119.3500	Shaw River, WA
U. saxatilis sp. nov.	WAM R114443		D	-20.6666	119.3500	Shaw River, WA
U. saxatilis sp. nov.	WAM R114444		D	-20.6666	119.3500	Shaw River, WA
U. saxatilis sp. nov.	WAM R114445		D	-20.6666	119.3500	Shaw River, WA
U. saxatilis sp. nov.	WAM R125726	Up0057	mt	-21.68440	116.33530	Robe River near Pannawonica, WA
U. saxatilis sp. nov.	WAM R125727	Up0058	mt	-21.68440	116.33530	Robe River near Pannawonica, WA
U. saxatilis sp. nov.	WAM R125728	Up0059	mt, n, M	-21.68440	116.33530	Robe River near Pannawonica, WA
U. saxatilis sp. nov.	WAM R125729		D	-21.6844	116.3353	Robe River near Pannawonica, WA
U. saxatilis sp. nov.	WAM R125743	Up0060	mt	-21.59440	117.06530	Millstream Water Authority Homestead, WA
U. saxatilis sp. nov.	WAM R125759	Up0061	mt	-21.59130	117.07250	Millstream Rangers Station, WA
U. saxatilis sp. nov.	WAM R125760	Up0062	mt, M	-21.59130	117.07250	Millstream Rangers Station, WA
U. saxatilis sp. nov.	WAM R125761	Up0063	mt	-22.64330	118.56310	Dale Gorge, Hamersley Ranges, WA
U. saxatilis sp. nov.	WAM R125762	Up0064	mt	-22.64330	118.56310	Dale Gorge, Hamersley Ranges, WA
U. saxatilis sp. nov.	WAM R125763	Up0065	mt	-22.64330	118.56310	Dale Gorge, Hamersley Ranges, WA
U. saxatilis sp. nov.	WAM R126647		D	-22.6433	118.5631	Dale Gorge, Hamersley Ranges, WA
U. saxatilis sp. nov.	WAM R135086	Up0090	mt, M	-22.25000	118.00000	Hamersley Gorge, Karijini National Park, WA
U. saxatilis sp. nov.	WAM R135087	Up0091	mt, M	-21.33330	117.20000	McKenzie Spring, Chichester Range National Park, WA
U. saxatilis sp. nov.	WAM R135371		D	-22.46	117.30	Mt. Brockman, WA
U. saxatilis sp. nov.	WAM R135636	Up0094	mt	-22.20	119.00	61 km NNE of Munjina Roadhouse, WA
U. saxatilis sp. nov.	WAM R135638	Up0096	mt, M	-21.48330	118.65000	Pinga Creek Crossing, WA
U. saxatilis sp. nov.	WAM R135639	Up0097	mt, M	-21.48330	118.65000	Pinga Creek Crossing, WA
U. saxatilis sp. nov.	WAM R135640		D	-21.4833	118.6500	Pinga Creek Crossing, WA
U. saxatilis sp. nov.	WAM R139147	Up0107	mt, M	-21.21630	120.34060	Meentheena, WA
U. saxatilis sp. nov.	WAM R140012	Up0106	mt, M	-21.18130	117.05780	Millstream-Chichester National Park, WA
U. saxatilis sp. nov.	WAM R145554	Up0108	mt, n, M	-20.78000	118.64000	53 km S of Port Hedland, WA
U. saxatilis sp. nov.	WAM R145558	Up0109	mt	-21.01000	118.70000	80 km S of Port Hedland, WA
U. saxatilis sp. nov.	WAM R145559	Up0110	mt, M	-21.01000	118.70000	80 km S of Port Hedland, WA
U. saxatilis sp. nov.	WAM R145561	Up0111	mt, M	-21.01000	118.70000	80 km S of Port Hedland, WA
U. saxatilis sp. nov.	WAM R145562		D	-21.0100	118.7000	80 km S of Port Hedland, WA

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. saxatilis sp. nov.	WAM R145563		D	-21.0100	118.7000	80 km S of Port Hedland, WA
U. saxatilis sp. nov.	WAM R145564		D	-21.0100	118.7000	80 km S of Port Hedland, WA
U. saxatilis sp. nov.	WAM R145678		D	-22.2500	119.0333	Abydos Station, WA
U. saxatilis sp. nov.	WAM R145711	Up0127	mt	-22.91660	119.21670	Weeli Wolli Creek, WA
U. saxatilis sp. nov.	WAM R145758	Up0128	mt	-21.94000	118.96080	Chichester Range, WA
U. saxatilis sp. nov.	WAM R154549	Up0130	mt, M	-23.38940	120.16140	Wheelarra Hill, WA
U. saxatilis sp. nov.	WAM R154550	Up0131	mt, M	-23.38940	120.16140	Wheelarra Hill, WA
U. saxatilis sp. nov.	WAM R154551	Up0132	mt, M	-23.38940	120.16140	Wheelarra Hill, WA
U. saxatilis sp. nov.	WAM R154552		D	-23.3894	120.1614	Wheelarra Hill, WA
U. saxatilis sp. nov.	WAM R154553		D	-23.3894	120.1614	Wheelarra Hill, WA
U. saxatilis sp. nov.	WAM R154554		D	-23.3894	120.1614	Wheelarra Hill, WA
U. saxatilis sp. nov.	WAM R154555		D	-23.3894	120.1614	Wheelarra Hill, WA
U. saxatilis sp. nov.	WAM R154627		D	-23.3894	120.1614	Wheelarra Hill, WA
U. saxatilis sp. nov.	WAM R154761		D	-23.3211	119.9378	Brockman Ridge, WA
U. saxatilis sp. nov.	WAM R154762		D	-23.3211	119.9378	Brockman Ridge, WA
U. saxatilis sp. nov.	WAM R154763		D	-23.3211	119.9378	Brockman Ridge, WA
U. saxatilis sp. nov.	WAM R154764	Up0136	mt, M	-23.31940	119.95330	Brockman Ridge, WA
U. saxatilis sp. nov.	WAM R156222	Up0137	mt, M	-20.60330	120.26420	Cattle Gorge, WA
U. saxatilis sp. nov.	WAM R156614	Up0147	mt, M	-21.64970	121.23810	Woodie Woodie Minesite, WA
U. saxatilis sp. nov.	WAM R161863		D	-21.4381	119.541	35.5 km SW of Marble Bar, WA
U. saxatilis sp. nov.	WAM R161893		D	-21.4381	119.541	35.5 km SW of Marble Bar, WA
U. saxatilis sp. nov.	WAM R162426		D	-20.8761	116.647	2 km NW of Karratha Station, WA
U. saxatilis sp. nov.	WAM R162770		D	-22.271	117.46	Mt. Brockman, WA
U. saxatilis sp. nov.	WAM R162771		D	-22.271	117.46	Mt. Brockman, WA
U. saxatilis sp. nov.	WAM R162772		D	-22.271	117.46	Mt. Brockman, WA
U. saxatilis sp. nov.	WAM R162774		D	-22.271	117.46	Mt. Brockman, WA
U. saxatilis sp. nov.	WAM R162838		D	-23.2839	118.102	45 km ESE of Paraburdoo, WA
U. saxatilis sp. nov.	WAM R162877	Up1061	mt, M	-23.34378	118.02128	Turee Creek, WA
U. saxatilis sp. nov.	WAM R163091		D	-22.89	119.22	Weeli Wolli Creek, WA
U. saxatilis sp. nov.	WAM R163092		D	-22.89	119.22	Weeli Wolli Creek, WA
U. saxatilis sp. nov.	WAM R163672		D	-22.6614	117.864	8km NE of Top Price, WA
U. saxatilis sp. nov.	WAM R163676		D	-22.7225	118.268	18.5 km SE of Mt. Bruce, WA

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. saxatilis sp. nov.	WAM R163677		D	-22.7225	118.268	18.5 km SE of Mt. Bruce, WA
U. saxatilis sp. nov.	WAM R163697		D	-22.7225	118.268	18.5 km SE of Mt. Bruce, WA
U. saxatilis sp. nov.	WAM R164597		D	-21.7083	116.766	15 km NNW of Mount Elvire, WA
U. saxatilis sp. nov.	WAM R165059		D	-21.5713	117.056	2.6 km NNW of Millstream, WA
U. saxatilis sp. nov.	WAM R165060		D	-21.5713	117.056	2.6 km NNW of Millstream, WA
U. saxatilis sp. nov.	WAM R165061		D	-21.5713	117.056	2.6 km NNW of Millstream, WA
U. saxatilis sp. nov.	WAM R165062		D	-21.5713	117.056	2.6 km NNW of Millstream, WA
U. saxatilis sp. nov.	WAM R165067		D	-21.5713	117.056	2.6 km NNW of Millstream, WA
U. saxatilis sp. nov.	WAM R166204	Up0148	mt	-21.95440	120.12170	10 km S of Nullagine, WA
U. saxatilis sp. nov.	WAM R166205		D	-21.9547	120.1264	10 km S of Nullagine, WA
U. saxatilis sp. nov.	WAM R166206	Up0149	mt, M	-21.95470	120.12640	10 km S of Nullagine, WA
U. talpa	WAM R10163		D	-20.5166	118.0500	Mundabullangana, WA
U. talpa	WAM R10164		D	-20.5166	118.0500	Mundabullangana, WA
U. talpa	WAM R22902		D	-20.5166	118.0500	Mundabullangana, WA
U. talpa	WAM R22903		D	-20.5166	118.0500	Mundabullangana, WA
U. talpa	WAM R22904		D	-20.5166	118.0500	Mundabullangana, WA
U. talpa	WAM R32172		D	-17.4333	123.7500	15 km S of Derby, WA
U. talpa	WAM R60848		D	-17.3833	122.1667	4 km SE of Coulomb Point, WA
U. talpa	WAM R60896		M	-17.3833	122.1667	4 km SE of Coulomb Point, WA
U. talpa	WAM R60897		D	-17.3833	122.1667	4 km SE of Coulomb Point, WA
U. talpa	WAM R60898		D	-17.3833	122.1667	4 km SE of Coulomb Point, WA
U. talpa	WAM R62472		D	-17.5833	123.7333	24–41 km S of Derby, WA
U. talpa	WAM R62473		D	-17.5833	123.7333	24–41 km S of Derby, WA
U. talpa	WAM R80525		D	-16.2500	123.5167	Hidden Island, Buccaneer Archipelago, WA
U. talpa	WAM R80526		D	-16.2500	123.5167	Hidden Island, Buccaneer Archipelago, WA
U. talpa	WAM R80527		D	-16.2500	123.5167	Hidden Island, Buccaneer Archipelago, WA
U. talpa	WAM R80528		D	-16.2500	123.5167	Hidden Island, Buccaneer Archipelago, WA
U. talpa	WAM R87305		M	-17.6333	123.7333	14 km NE of Willare Bridge Roadhouse, WA
U. talpa	WAM R88534		D	-19.7333	121.4667	55 km S of Anna Plains Homestead, WA
U. talpa	WAM R94430		D	-17.3833	123.6833	10 km SSE of Derby, WA
U. talpa	WAM R94431		M	-17.4666	123.7500	22 km SE of Derby, WA
U. talpa	WAM R94432		D	-17.4666	123.7500	22 km SE of Derby, WA
U. talpa	WAM R94433		D	-17.4666	123.7500	22 km SE of Derby, WA
U. talpa	WAM R94434		D	-17.4666	123.7500	22 km SE of Derby, WA
U. talpa	WAM R94436		M	-17.9000	122.2667	8 km NE of Broome, WA
U. talpa	WAM R94437		M	-17.9000	122.2667	8 km NE of Broome, WA
U. talpa	WAM R94438		M	-17.9000	122.2667	8 km NE of Broome, WA
U. talpa	WAM R94439		D	-17.6500	123.1333	106 km E of Broome, WA
U. talpa	WAM R94440		D	-17.6500	123.1333	106 km E of Broome, WA
U. talpa	WAM R97123		D	-17.3000	123.6167	Derby, WA
U. talpa	WAM R97124		D	-17.3000	123.6167	Derby, WA
U. talpa	WAM R112649		M	-16.6833	123.8333	Kimbolton Station, WA
U. talpa	WAM R112981	Up0124	mt, n	-17.05250	122.76250	Beagle Bay Aboriginal Community, WA
U. talpa	WAM R135162	Up0092	mt	-17.85000	122.73330	Lake Campion, WA

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APPENDIX 1. (continued)

Species	Museum ID	Lab ID	Data	Latitude	Longitude	Location
U. talpa	WAM R135641	Up0098	mt, M	-20.50000	118.36670	32 km SW of Port Hedland, WA
U. talpa	WAM R135642	Up0099	mt, M	-20.50000	118.36670	32 km SW of Port Hedland, WA
U. talpa	WAM R135643	Up0100	mt, n, M	-20.50000	118.36670	32 km SW of Port Hedland, WA
U. talpa	WAM R135644	Up1059	mt, M	-20.5000	118.3667	32 km SW of Port Hedland, WA
U. talpa	WAM R135645	Up1060	mt, M	-20.5000	118.3667	32 km SW of Port Hedland, WA
U. talpa	WAM R135894		D	-20.5000	118.3667	32 km SW of Port Hedland, WA
U. talpa	WAM R139088		M	-19.8122	121.4736	Mandora, WA
U. talpa	WAM R139093		M	-19.8083	121.4639	Mandora, WA
U. talpa	WAM R151774	Up0125	mt, M	-17.05250	122.76250	Beagle Bay Aboriginal Community, WA
U. talpa	WAM R161205	Up0145	mt, M	-17.18220	122.83780	37.7 km E of Roebuck Roadhouse, WA
U. talpa	WAM R161206	Up0146	mt, M	-17.18220	122.83780	37.7 km E of Roebuck Roadhouse, WA
U. talpa	WAM R161232		D	-20.5256	118.077	45 km NNE of Whim Creek Hotel, WA
U. talpa	WAM R163242		D	-17.9666	122.2333	Broome Area, WA
U. talpa	WAM R1639		D	-20.1833	119.1833	De Gray Station, WA
U. talpa	WAM R164649	Up0233	mt, M	-17.7308	123.5614	Fitzroy floodplain S. Derby (Cockatoo Creek), WA
U. talpa	WAM R164650	Up0234	mt, M	-17.7308	123.5614	Fitzroy floodplain S. Derby (Cockatoo Creek), WA
U. talpa	WAM R164651	Up0235	mt, M	-17.7308	123.5614	Fitzroy floodplain S. Derby (Cockatoo Creek), WA
U. talpa	WAM R164672	Up0241	mt, M	-17.8280	124.2653	65km E of junction between Great Northern Hwy and Derby Rd, WA
U. talpa	WAM R164673	Up0242	mt, M	-17.8280	124.2653	65km E of junction between Great Northern Hwy and Derby Rd, WA
U. talpa	WAM R164734	Up0257	mt, n, M	-18.1091	125.4353	13 km W of Fitzroy Crossing, WA
U. talpa	WAM R164739	Up0262	mt, M	-18.1091	125.4353	13 km W of Fitzroy Crossing, WA
U. talpa	WAM R164740	Up0263	mt, M	-18.1091	125.4353	13 km W of Fitzroy Crossing, WA
U. talpa	WAM R166487	Up0151	mt, M	-20.34330	119.12000	60 km E of Port Hedland, WA
U. talpa	WAM R166490	Up0153	mt, M	-20.34330	119.12000	60 km E of Port Hedland, WA
U. trachyderma	SAMA ABTC12494	Up1026	mt, n	-17.4825	135.651	Tableland Hwy, NT
U. tyleri	this study	Up0011	mt, n	-35.16070	150.66510	Ryan's Swamp, Jervis Bay, NSW

Appendix 2: Genbank Accession numbers for *Uperoleia* mitochondrial genes.

Species	Museum ID	Lab ID	16S	ND2
Spicospina flammocaerulea	SAMA ABTC69165	Myo121	JF263329	JF263218
U. altissima	QM N75766	Up0400	JF263420	JF263308
U. aspera	WAM R164676	Up0245	JF263414	JF263302
U. borealis	WAM R162484	Up0162	JF263404	JF263292
U. crassa	WAM R167727	Up0193	JF263405	JF263293
U. fusca	this study	Up0056	JF263332	JF263220
U. glandulosa	WAM R115638	Up0085	JF263346	JF263234
U. glandulosa	WAM R115639	Up0086	JF263347	JF263235
U. glandulosa	WAM R135637	Up0095	JF263355	JF263243
U. glandulosa	WAM R135900	Up0102	JF263361	JF263249
U. glandulosa	WAM R135901	Up0103	JF263362	JF263250
U. glandulosa	WAM R154273	Up0129	JF263386	JF263274
U. glandulosa	WAM R166488	Up0152	JF263401	JF263289
U. inundata	NTM R35103	Up0270	JF263418	JF263306
U. laevigata	this study	Up0040	JF263331	JF263219
U. lithomoda	WAM R162466	Up0157	JF263403	JF263291
U. littlejohni	this study	Up0394	JF263419	JF263307
U. micra	WAM R168039	Up0220	JF263407	JF263295
U. micromeles	SAMA ABTC12487	Up0790	JF263431	JF263319

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Appendix 2. (continued)

Species	Museum ID	Lab ID	16S	ND2
U. micromeles	SAMA ABTC12488	Up0791	JF263432	JF263320
U. micromeles	SAMA ABTC12490	Up0792	JF263433	JF263321
U. micromeles	SAMA ABTC12491	Up0793	JF263434	JF263322
U. micromeles	SAMA ABTC12492	Up0795	JF263435	JF263323
U. micromeles	SAMA ABTC12493	Up0796	JF263436	JF263324
U. micromeles	WAM R115640	Up0087	JF263348	JF263236
U. micromeles	WAM R115641	Up0088	JF263349	JF263237
U. micromeles	WAM R137913	Up0104	JF263363	JF263251
U. minima	WAM R167878	Up0201	JF263406	JF263294
U. mjobergi	WAM R164619	Up0230	JF263408	JF263296
U. rugosa	SAMA ABTC03645	Up0606	JF263421	JF263309
U. russelli	SAMA ABTC11689	Up0745	JF263422	JF263310
U. russelli	SAMA ABTC11690	Up0746	JF263423	JF263311
U. russelli	SAMA ABTC11691	Up0747	JF263424	JF263312
U. russelli	SAMA ABTC11692	Up0748	JF263425	JF263313
U. russelli	SAMA ABTC11693	Up0749	JF263426	JF263314
U. russelli	SAMA ABTC11733	Up0750	JF263427	JF263315
U. russelli	SAMA ABTC11734	Up0751	JF263428	JF263316
U. russelli	SAMA ABTC11735	Up0752	JF263429	JF263317
U. russelli	SAMA ABTC11736	Up0753	JF263430	JF263318
U. russelli	WAM R112535	Up0112	JF263371	JF263259
U. russelli	WAM R112536	Up0113	JF263372	JF263260
U. russelli	WAM R112540	Up0114	JF263373	JF263261
U. russelli	WAM R112547	Up0115	JF263374	JF263262
U. russelli	WAM R112548	Up0116	JF263375	JF263263
U. russelli	WAM R112560	Up0118	JF263376	JF263264
U. russelli	WAM R112565	Up0119	JF263377	JF263265
U. russelli	WAM R112585	Up0120	JF263378	JF263266
U. russelli	WAM R112586	Up0121	JF263379	JF263267
U. russelli	WAM R112587	Up0122	JF263380	JF263268
U. russelli	WAM R117696	Up0123	JF263381	JF263269
U. russelli	WAM R135077	Up0089	JF263350	JF263238
U. russelli	WAM R138091	Up0105	JF263364	JF263252
U. saxatilis sp. nov.	WAM R100660	Up0081	JF263344	JF263232
U. saxatilis sp. nov.	WAM R100661	Up0082	JF263345	JF263233
U. saxatilis sp. nov.	WAM R102198	Up0072	JF263342	JF263230
U. saxatilis sp. nov.	WAM R110881	Up0138	JF263392	JF263280
U. saxatilis sp. nov.	WAM R110882	Up0139	JF263393	JF263281
U. saxatilis sp. nov.	WAM R110883	Up0140	JF263394	JF263282
U. saxatilis sp. nov.	WAM R125726	Up0057	JF263333	JF263221
U. saxatilis sp. nov.	WAM R125727	Up0058	JF263334	JF263222
U. saxatilis sp. nov.	WAM R125728	Up0059	JF263335	JF263223
U. saxatilis sp. nov.	WAM R125743	Up0060	JF263336	JF263224
U. saxatilis sp. nov.	WAM R125759	Up0061	JF263337	JF263225
U. saxatilis sp. nov.	WAM R125760	Up0062	JF263338	JF263226
U. saxatilis sp. nov.	WAM R125761	Up0063	JF263339	JF263227
U. saxatilis sp. nov.	WAM R125762	Up0064	JF263340	JF263228
U. saxatilis sp. nov.	WAM R125763	Up0065	JF263341	JF263229
U. saxatilis sp. nov.	WAM R135086	Up0090	JF263351	JF263239
U. saxatilis sp. nov.	WAM R135087	Up0091	JF263352	JF263240
U. saxatilis sp. nov.	WAM R135636	Up0094	JF263354	JF263242
U. saxatilis sp. nov.	WAM R135638	Up0096	JF263356	JF263244
U. saxatilis sp. nov.	WAM R135639	Up0097	JF263357	JF263245
U. saxatilis sp. nov.	WAM R139147	Up0107	JF263366	JF263254
U. saxatilis sp. nov.	WAM R140012	Up0106	JF263365	JF263253
U. saxatilis sp. nov.	WAM R145554	Up0108	JF263367	JF263255

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Appendix 2. (continued)

Species	Museum ID	Lab ID	16S	ND2
U. saxatilis sp. nov.	WAM R145558	Up0109	JF263368	JF263256
U. saxatilis sp. nov.	WAM R145559	Up0110	JF263369	JF263257
U. saxatilis sp. nov.	WAM R145561	Up0111	JF263370	JF263258
U. saxatilis sp. nov.	WAM R145711	Up0127	JF263384	JF263272
U. saxatilis sp. nov.	WAM R145758	Up0128	JF263385	JF263273
U. saxatilis sp. nov.	WAM R154549	Up0130	JF263387	JF263275
U. saxatilis sp. nov.	WAM R154550	Up0131	JF263388	JF263276
U. saxatilis sp. nov.	WAM R154551	Up0132	JF263389	JF263277
U. saxatilis sp. nov.	WAM R154764	Up0136	JF263390	JF263278
U. saxatilis sp. nov.	WAM R156222	Up0137	JF263391	JF263279
U. saxatilis sp. nov.	WAM R156614	Up0147	JF263397	JF263285
U. saxatilis sp. nov.	WAM R162877	Up1061	JF263440	JF263328
U. saxatilis sp. nov.	WAM R166204	Up0148	JF263398	JF263286
U. saxatilis sp. nov.	WAM R166206	Up0149	JF263399	JF263287
U. saxatilis sp. nov.	WAM R90922	Up0079	JF263343	JF263231
U. talpa	WAM R112981	Up0124	JF263382	JF263270
U. talpa	WAM R135162	Up0092	JF263353	JF263241
U. talpa	WAM R135641	Up0098	JF263358	JF263246
U. talpa	WAM R135642	Up0099	JF263359	JF263247
U. talpa	WAM R135643	Up0100	JF263360	JF263248
U. talpa	WAM R135644	Up1059	JF263438	JF263326
U. talpa	WAM R135645	Up1060	JF263439	JF263327
U. talpa	WAM R151774	Up0125	JF263383	JF263271
U. talpa	WAM R161205	Up0145	JF263395	JF263283
U. talpa	WAM R161206	Up0146	JF263396	JF263284
U. talpa	WAM R164649	Up0233	JF263409	JF263297
U. talpa	WAM R164650	Up0234	JF263410	JF263298
U. talpa	WAM R164651	Up0235	JF263411	JF263299
U. talpa	WAM R164672	Up0241	JF263412	JF263300
U. talpa	WAM R164673	Up0242	JF263413	JF263301
U. talpa	WAM R164734	Up0257	JF263415	JF263303
U. talpa	WAM R164739	Up0262	JF263416	JF263304
U. talpa	WAM R164740	Up0263	JF263417	JF263305
U. talpa	WAM R166487	Up0151	JF263400	JF263288
U. talpa	WAM R166490	Up0153	JF263402	JF263290
U. trachyderma	SAMA ABTC12494	Up1026	JF263437	JF263325
U. tyleri	this study	Up0011	JF263330	JF263217